

FISHERIES RESEARCH BOARD OF CANADA

Biological Station, Nanaimo, B.C.

1908-1958

BY A. W. NEEDLER, DIRECTOR

IN 1958 the Fisheries Research Board of Canada's Biological Station at Nanaimo, British Columbia, celebrates its fiftieth anniversary. From small beginnings in 1908 it has become one of the large, active fisheries research units of the world. In its early years the Station had no year-round staff. Its work was carried on by visiting scientists, mainly in the summer, and, though of much fundamental value, was restricted in scope. The Station has now grown until its research activities extend the length of the British Columbia coast and from far in the interior to the mid-Pacific. In this work it employs a hundred scientists and technicians the year round and about half that number seasonally, and operates several vessels and field stations.

ESTABLISHMENT OF THE STATION

The value of scientific knowledge to the maintenance and development of fisheries was from the first the key-note of the proposals to establish biological stations in Canada. The latter half of the nineteenth century was a period of imagination and adventure in the study of the sea. The epoch-making voyage of H.M.S. *Challenger* in 1872-1876 to study the physical characteristics and the life of the world's great oceans, and the establishment of the first great marine biological laboratory at Naples in 1872 were but two examples. Especially in northern Europe, much attention was turned to learning about the commercial fishes, and the economic value of fisheries research was stressed. In 1899 the International Council for the Exploration of the Sea was formed to coordinate the great volume of research by the European countries, and became the first international body with the expressed purpose of benefitting the fisheries.

Interest in the study of the sea and its fisheries also developed in Canada during this period. As early as 1884 a paper by James Playfair McMurich, later to become a chairman of the Biological Board of Canada (precursor of the Fisheries Research Board), advocated the establishment of stations for scientific studies to assist fisheries development. The Department of Marine and Fisheries in 1892 appointed Mr. E. E. Prince of St. Andrew's Marine Laboratory, Scotland, as Commissioner and General Inspector of Fisheries for Canada. He brought with him knowledge of marine research in Europe and became a strong advocate of marine biological stations for Canada. Support also came from the Royal Society of Canada which, in a resolution in 1896, urged the Government to implement Mr. Prince's proposals. Finally in 1898 \$7,000 was appropriated to build a station on the Atlantic coast and operate it for one year. A Board of Management of the

Marine Biological Station of Canada was appointed, with the Commissioner of Fisheries, Mr. Prince, representing the Government. This Board, later to become the Biological Board of Canada by Act of Parliament in 1912, built a floating station in 1899 and operated it at St. Andrews, N.B., Canso, N.S., Malpeque, P.E.I., and Gaspé, Quebec, before building a permanent station at St. Andrews in 1908.

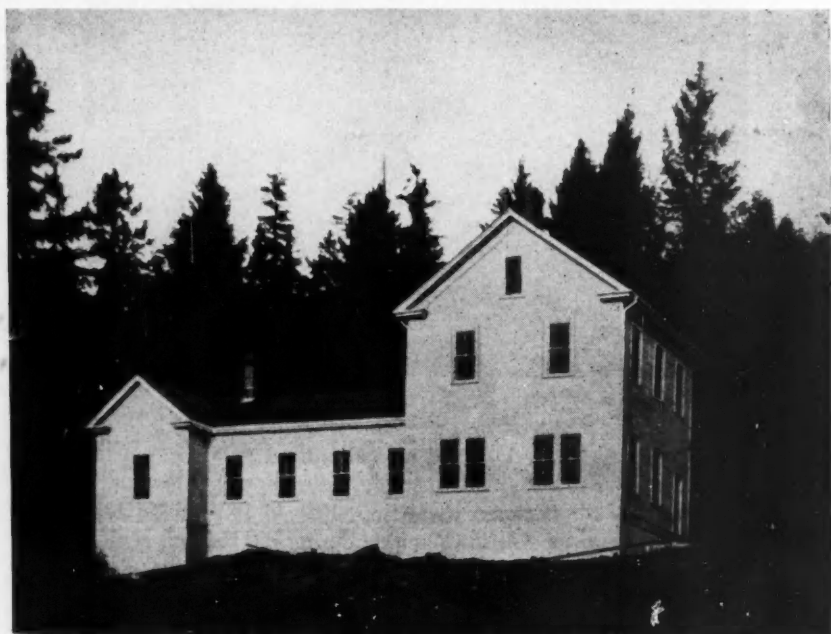


The Reverend George W. Taylor. A strong advocate of the establishment of the Station and its first Director, 1908 to 1912.

The Reverend George W. Taylor, a naturalist and a Fellow of the Royal Society of Canada, played an active part in the establishment of the Pacific coast station. He was a member of the federal government's British Columbia Fisheries Commission, which was appointed in 1905, with Mr. Prince as chairman, to consider the many pressing problems of the province's fisheries, then in a stage of very active development. In its interim report in 1905 the Commission emphasized that its work was hampered by lack of information and recommended action to initiate scientific investigations. The proposal was endorsed by the Vancouver Board of Trade and urged in Parliament in 1907 by Mr. William Sloan, M.P. Mr. Taylor presented a strong case for the establishment of a Station

in a paper which appears in the Transactions of the meeting of the Royal Society of Canada in June 1907. Provision for the construction of a Station on the Pacific coast was included in the funds voted by Parliament in 1907 for the construction and maintenance of marine biological stations and investigations in Canada. The British Columbia Fisheries Commission expressed the belief that the new Station would "prove of the very greatest value to the fishery industries of Canada".

The Board of Management of the Biological Station appointed a sub-committee to select a site, and a number of localities were examined. A central position among Strait of Georgia fishing grounds, a local herring fishery, good shelter and accessibility from Vancouver and Victoria commended the Nanaimo area on Vancouver Island. Land was acquired at Departure Bay and the new Station was made ready for use in the summer of 1908.



The first Station building soon after its completion in 1908.

EARLY YEARS OF THE STATION

The laboratory built in 1908 could accommodate about eight scientists. It had running fresh and salt water but, of course, no electricity. Space was provided for office, library, photographic dark-room and, upstairs, four bedrooms for visiting scientists which were supplemented, as occasion demanded, with tents. An adjoining building housed kitchen and caretaker's quarters. Small boats were available for collecting specimens and observations.

The Reverend George W. Taylor was in charge of the Station until his death in August, 1912, his deep interest in its work persisting until the end. He was succeeded by Dr. C. McLean Fraser, who had spent several seasons in the Board's



Dr. C. McLean Fraser. Director, 1912 to 1924.

work on both coasts and who remained in charge until 1924. During this period the Station had no year-round scientific employees except the Director, and even Dr. Fraser spent only the summers there from 1920 to 1924, being Professor of Zoology at the University of British Columbia during the balance of those years. The research at the Station was carried out mainly by university scientists who visited it during the summers.

This was a period of active research in many branches of biology. Studies were carried out on the occurrence and life histories of many different kinds of marine animals and plants. The Station was also used for research on the chemistry and physiology of fishes and marine invertebrates. It was even used as a base for studies of land plants and animals and of geology; but most of the work was, of course, concerned with marine plants and animals, how they are constituted and how they live, reproduce and react with their environment. Work was carried out which was of very considerable general scientific value and, at the same time, essential background was provided for later researches aimed more directly at solution of fisheries problems. Nor were these themselves neglected. The subjects studied included many of immediate economic interest,

such as the reproduction and growth of salmon, halibut, herring and other commercial fish and shellfish, physical and chemical conditions in the sea and their effects on the movements of fish and other marine animals, marine wood borers, sea lions and potentially valuable seaweeds.

Most of the scientists who worked at the Station came from Canadian universities, some from the United States or even Europe. Many were then eminent in their fields; others were younger and had yet to make their names. All worked, without remuneration other than expenses, for the satisfaction that comes from scientific discovery and the development and exchange of new ideas. The individual scientists were interested in their own problems and usually continued to work on them after returning to their universities.

This association of university scientists with the work of the Station continued for some time after the development of its full-time scientific staff in the years following 1924. Scarcity of funds in the great economic depression of the 1930's and concentration of the Station's resources on specific fisheries investigations by its own employees combined to discourage the voluntary and relatively independent work of university scientists at the Board's stations. Those university workers who have taken part in the great development of the fisheries investigations in recent years have done so as paid seasonal employees on specific projects which are part of the program of the Fisheries Research Board. Although facilities can be made available for visiting scientists to work on their own problems, few now feel that they can afford to come without remuneration.

The association of the two groups of scientists was stimulating and valuable. Senior university scientists with their own active interests contributed experience and ideas from which the Station's work and employees gained much. Graduate students spending summers at the Station developed interest and ability in the solution of fisheries problems and many of the Board's most valuable employees started in this way. The university scientists gained stimulating contacts with other research workers and with living animals, as well as facilities for their work. It is hoped that the Station's contacts with independent university research can again be strengthened.

EXPANSION OF FISHERIES INVESTIGATIONS IN THE 1920'S AND 1930'S

In the middle 1920's there was a strong surge of interest in research on practical fisheries problems. One of its manifestations was the establishment of technological stations to study the problems of processing and transporting fish; another was the great expansion of the work of the biological stations on the two coasts. A year-round scientific staff was built up and facilities were greatly improved in order to carry out a research program which included for the first time major long-term investigations of fisheries problems.

At the Nanaimo Station this expansion was carried out under Dr. W. A. Clemens, who was Director from 1924 until 1940, when he resigned to head the Zoology Department of the University of British Columbia and was replaced by Dr. R. E. Foerster.



Dr. W. A. Clemens. Director, 1924 to 1940.

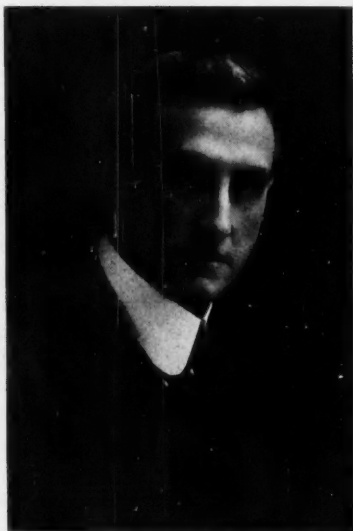
A small chemistry laboratory had been built in the winter of 1923-24, but Dr. Clemens was faced with the problem of providing more adequate quarters for the growing staff and many visiting scientists. A bungalow for the Director and a cottage for the caretaker were built in 1925, releasing working space in the older buildings. A three-storey frame building was completed in 1928 to provide living quarters for visiting scientists and some of the junior members of the scientific staff. This has since been converted to working space.

In 1926 a small vessel, named the *A. P. Knight* after the recently retired Chairman of the Board, was built by the Department of Fisheries for the Station's use. Though neither designed nor equipped as a fishing vessel, it served the Station well for oceanographic observations, scientific collections and transportation of personnel in inshore waters, until 1947.

Starting with two appointments in 1926, the year-round scientific staff was increased to eleven in 1932 and remained at about that level until the end of World War II. Many of the scientists employed at that time have since moved on to important posts elsewhere in Canada and the United States.



The Station in 1925. A chemistry laboratory (left) and a concrete basement for the first building were completed in 1924.



Mr. and Mrs. C. J. Berkeley, who have been active volunteer research scientists at the Station from 1919 to the present time. Mrs. Berkeley has specialized in the study of marine polychaete worms; Mr. Berkeley has conducted a variety of studies, mainly on invertebrates.



The Station's research vessel *A. P. Knight*, 1926 to 1947, here at work in Princess Louisa Inlet, was equipped for dredging and general biological and oceanographic investigations in inshore waters.



A group of scientists at the Station in 1927. Seated: left, Dr. Clemens, Director; right, Dr. D. B. Finn, then Director of the Board's Technological Station at Prince Rupert, now head of the Fisheries Division of the Food and Agricultural Organization of the United Nations. Standing: left to right, Dr. C. H. Williamson, Mr. G. H. Wailes, Mr. Louis Smith, Dr. H. N. Brocklesby, Dr. R. E. Foerster, later Director of the Station, 1940 to 1950.



Some members of the scientific staff in 1938. Left to right: Dr. D. B. Quayle (later in charge of the Province of British Columbia's Shellfish Laboratory), Dr. W. A. Clemens, Director (recently retired as head of the Zoology Department, University of British Columbia), Dr. A. L. Tester (now Chief, Division of Biological Research, United States Fish and Wildlife Service), Dr. W. M. Cameron (now Director of Scientific Services, Royal Canadian Navy), Dr. J. L. Hart (now Director of the Fisheries Research Board's Biological Station, St. Andrews, N.B.), Dr. J. L. McHugh (now Director, Virginia Fisheries Laboratory), Dr. A. L. Pritchard (now Director, Conservation and Development Service, Department of Fisheries, Ottawa).

The research program of the Station was influenced by the state of knowledge and the special problems of the day. Over a period of six years, intensive long-term studies were started on salmon propagation and migration, on herring and pilchards, on oysters and other shellfish, on trout propagation and on oceanography. From this period onward the work of the Station has been more and more directly concerned with pressing fisheries problems.

In 1926 an intensive study of the relative efficiency of natural and artificial propagation of sockeye salmon was commenced at Cultus Lake, tributary to the lower Fraser River, under Dr. R. E. Foerster who had been studying conditions in the lake as a graduate student since 1922. The numbers of young seaward migrants from the lake resulting from known numbers of eggs under natural conditions were compared with those resulting from two fish-culture techniques applied with the cooperation of the Department of Fisheries. The thoroughness of this experiment, continued over eight broods, made it a classic in the field of salmon research. It demonstrated for the first time the high mortality in the early stages of salmon development. Its failure to show advantages from the existing fish culture techniques commensurate with their costs led to the closure of the salmon hatcheries in British Columbia. Other important studies on sockeye salmon reproduction were associated with this program.

A program of tagging salmon to reveal their migrations in the sea was also commenced in 1926 and continued for a number of years. It gave us our first firm information on the coastwise movements of spring and coho salmon.

In 1930 a major investigation of the production of pink salmon was commenced. At Masset Inlet in the Queen Charlotte Islands the numbers of fry resulting from known numbers of eggs, and the factors responsible for mortalities from egg to fry stage, were studied using a counting fence on McClinton Creek to enumerate fry and adults. Attempts were made without success to establish runs of pink salmon in the alternate years when none occur naturally in that area.

Research on trout production, then a responsibility of the federal government, was started in a preliminary way in 1928 and expanded in 1930. It included studies on hatchery rearing of Kamloops trout and their introduction into a small under-populated lake in the interior. Work on the reproduction of rainbow and brown trout, and on Atlantic, spring and coho salmon was conducted at Cowichan Lake, where the hatchery was turned over to the station for experimental purposes.

Intensive study of herring and pilchard was commenced in 1929, and investigations on which to base regulation of the important herring fishery still form an important part of the Station's program. The early work established the pattern of herring movements and the divisions of the stock, and laid the groundwork for intensive quantitative studies on herring production. The pilchard investigations demonstrated that the British Columbia fishery depended on older fish which were part of the larger California stocks. Their serious decline in 1942 affected both areas and brought the Canadian fishery and research on this species to an end.

Following earlier preliminary investigations, an intensive program of research on oyster culture was started in 1930 and expanded to include study of the clam stocks and fishery. Investigations were also carried out on the crab fishery, on prawns, and on marine borers. Other projects included studies on the food of fur seals, on sea lions, and on lingcod.

The above illustrates the increasing attention paid to problems of significance to fisheries. In these studies there was close co-operation both with branches of the Canadian Department of Fisheries and with the Provincial Government, which contributed financially to some projects.

The need for knowledge of oceanographic conditions, so important to an understanding of the movements and fluctuating abundance of fish, was not forgotten during this period. An oceanographic study of the Strait of Georgia was carried out by scientists of the University of British Columbia for a number of summers starting in 1926. Two full-time oceanographers joined the Station's staff in 1930 and 1931.

An interesting development was the construction of a hydraulic model of Alberni Inlet to study the circulation. Using dyes to colour water layers having different salinity and to indicate their movements, it was possible to determine the circulation at various levels of river discharge. Results were checked by actual observations in the inlet. As a result the dispersion pattern of pulp-mill effluents



The Station in 1944 showing, from left to right, the annex first built as a residence in 1928, the Director's house, the boat house and workshop (at foot of wharf), the chemistry laboratory, and the original station building. The research vessel *A. P. Knight* is at the wharf.

in the inlet was predicted and effective measures to prevent damage to fisheries were recommended and carried out.

THE STATION DURING WORLD WAR II

During the early years of the war the work of the Station proceeded at a somewhat reduced rate, owing to absence of scientific staff on war service. It was possible, however, to continue to accumulate knowledge applicable to the maintenance and development of our fisheries.

The outstanding feature of the war years was the development of co-operation with the Royal Canadian Navy in oceanographic research. The Station provided scientific personnel not available elsewhere, and the Navy provided ships. The joint effort was very effective in getting useful information for defence purposes. It laid the basis for increasingly useful co-operation along the same lines in the post-war period. The information needed by Navy as a basis for submarine detection, and that needed to understand the abundance and movements of fish, coincide to a very high degree. With this background, our knowledge of the pattern of oceanographic conditions and circulation has advanced so far in the last few years that we are looking forward to the day when we can predict changes in the sea and resulting changes in size of fish stocks and in the timing and course of their movements. This day is still in the future but when it comes it will mark an extremely important advance in fisheries management and exploitation.

POST-WAR DEVELOPMENT

Commencing in the last years of the war the Station's research program, staff and facilities have grown steadily and rapidly in response to strong demands for work on domestic and international fisheries problems.

The year-round scientific staff increased from 12 in 1943 to 46 in 1958 and is now assisted by 55 technicians and 32 clerical, maintenance and vessel personnel. About 50 seasonal scientists and technicians are also employed in the Station's research. Dr. R. E. Foerster was succeeded as Director by Dr. J. L. Hart in 1950. An exchange of Directors between the Fisheries Research Board's biological stations at Nanaimo and at St. Andrews, N.B., brought the writer to the Station in 1954.

To keep pace with growing needs for working space, a four-storey concrete laboratory was completed in 1949 on the site of the original 1908 frame building. A two-storey concrete workshop was built in 1950, replacing an older frame structure, and a third storey was added in 1955 to house work on electronic equipment. In spite of these additions it has become necessary to use all of the former residence building for scientific work and to seek further laboratory space by re-arrangement of the main building.

The Station acquired the 54-foot dragger *Investigator No. 1* in 1946 and the 39-foot troller *Alta* in 1952. A modern 76-foot multi-purpose fishing vessel was purchased in 1958 and re-named *A. P. Knight*, after the Station's first research vessel. Many other vessels, mainly commercial fishery, have been chartered from time to time for special purposes.



The dragger *Investigator No. 1* bought by the Station in 1946 and still in active use in herring, groundfish and other investigations.

It is possible to mention only some of the principal new projects in this post-war period of very active development.

The war itself, through creation of a demand for bottom fish and consequently an otter-trawl fishery, stimulated work in a new field. Fears of over-fishing, which seem to have some justification in the case of certain species, led to the initiation in 1943 of a program including statistical study of the fishery, sampling of the more important groundfish stocks and study of their life histories and migrations, in order to provide the basis for regulation as required. Desirability of co-ordinating regulations governing Canadian and United States fishing of the same stocks has recently involved some co-operative studies.

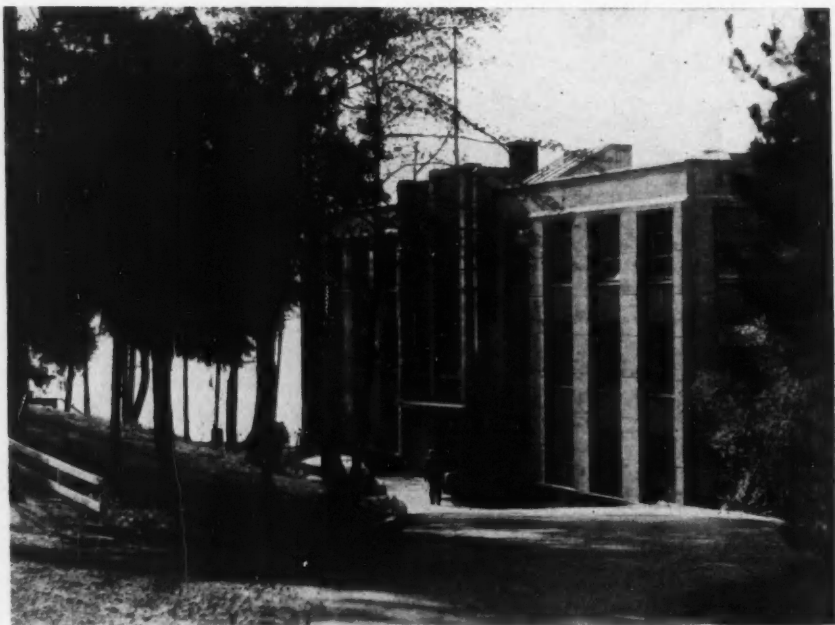
The salmon fisheries are the most important on the Pacific coast and attention has, of course, been given to improving the basis for their management. The sockeye, and more recently the pink, salmon of the Fraser River have been studied by the International Pacific Salmon Fisheries Commission but many other salmon stocks present problems, and those of the Skeena River system have been specially important. A survey of this system in 1944-48 provided valuable background. Since 1955, investigations have been intensified in connection with the Skeena River Salmon Management Committee through which the federal department's Area Director of Fisheries and the Director of the Station combine resources to learn how to obtain the best yield from the fishery. To determine how many spawners should be allowed to escape the fishery, studies are made of the



A counting fence completed in 1946 at the outlet of Babine Lake, the principal sockeye salmon nursery of the Skeena River system. Salmon on their way to the spawning grounds approach the fence from the left; they are counted, sampled and examined for tags as they leave the five traps on the right.

numbers of young seaward migrants produced by various numbers of spawners and of the capacities of streams and lakes to incubate the eggs and rear the young. To determine how to regulate the fishery to let the needed spawners pass, salmon are tagged to discover the routes and timing of various runs, proportions caught by the fishery are closely studied and special gill-netting is carried out just above the up-river boundary of fishing to get early enough information on the numbers getting through to permit adjustment of regulations if desirable. In these ways progress is being made towards making the best use of the Skeena salmon resource. Efforts to improve the basis for regulation of the fishery are being extended to other stocks as resources permit.

Population growth and industrialization offer serious threats to salmon production through pollution, through diversion of water to other uses and through obstructions such as dams for hydro-electric power. The Station has been paying increasing attention to solution of the difficult and complex problems involved in the attempt to maintain our fisheries in the face of these developments. Individual cases of actual or threatened pollution are studied to learn how to dispose of domestic or industrial wastes with the least possible damage to fisheries, and the toxicities of particular pollutants are studied and means sought for rendering them innocuous. An experimental study of the capacities and reactions of salmon was started in 1950 with the principal aim of learning how to guide them past obstructions. This work was concentrated first on the problems of getting young



The main building of the Station, completed in 1949 on the site of the original 1908 structure.



The 39-foot troller *Alta* acquired by the Station in 1952 for salmon investigations.

salmon safely down to sea, and progress has been made towards this objective. More recently attention has been turned to adult salmon and a major study of their physiology and behaviour is in progress, still aimed at discovering what stresses they can stand, how they behave under various conditions and how their capacities and reactions can be used to get them past obstructions without impairing their potential as spawners.

In association with these "defensive" attempts to maintain salmon stocks in spite of population increase, industrialization, and ever-increasing fishing power, a positive approach has not been forgotten. Work has proceeded on artificial means of increasing the numbers of salmon. Investigations have been carried out on the conditions required for the incubation of salmon eggs and on their occurrence in the gravel beds where salmon spawn. Practical means of assuring conditions under which larger numbers of eggs will survive are being explored. Hatcheries have long been able to incubate a much higher proportion of salmon

eggs than does Nature, but the resulting fry have not usually survived well enough to achieve any over-all gain. Experiments are in progress on the improvement of techniques of hatching and releasing fry in the light of recent advances in knowledge of the behaviour and physiology of young salmon. Artificial propagation of salmon has great potentialities if its many challenging problems can be solved, and the Station is becoming increasingly active in this field.

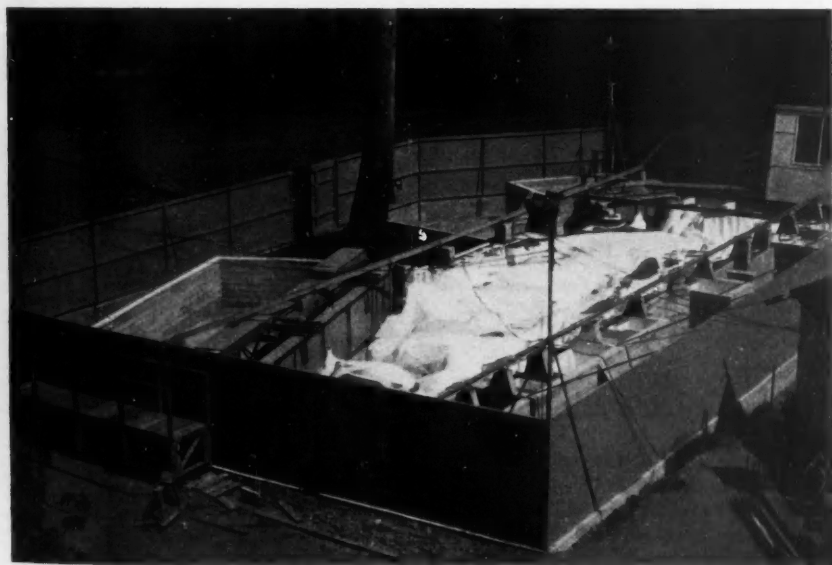
In 1953 Canada, Japan and United States ratified a treaty which established the International North Pacific Fisheries Commission and led to one of the world's greatest co-operative fisheries investigations. The Station has carried out Canada's share in a research program to discover where salmon originating in various rivers in North America and Asia go in the North Pacific. Exploratory fishing has shown that salmon are widely distributed on the high seas and has provided samples for comparison with others taken in inshore and fresh waters. The Station has played an active part in the high-seas fishing and inshore



The Station in 1957. At the left is the annex built in 1928 as a residence for summer workers but now used for research. To its right is the Director's house (partly hidden by trees), then the 3-storey concrete workshop, the small chemistry laboratory built in 1924, and the main building. Behind the main building is a storehouse and the caretaker's cottage, the latter mostly concealed. A model of Hecate Strait is under construction in the cleared space above the main building. The house in the woods at the right was built by the first Director, the Reverend G. W. Taylor. In the right foreground are the "Black Rocks".

sampling, and in studies of parasites, scales and other characteristics of salmon. These studies have shown that salmon originating in various river systems mix over wide areas of the North Pacific only to separate again and return as spawning adults to their native streams. These investigations have carried the Station's work to mid-ocean and are greatly increasing our knowledge not only of the distribution of salmon stocks but also of the North Pacific and its potential resources generally. A particularly promising by-product of this work is an ever-increasing insight into the pattern of oceanographic conditions and their changes, by which we hope to understand and perhaps eventually to predict changes in existing fisheries, and to discover new ones.

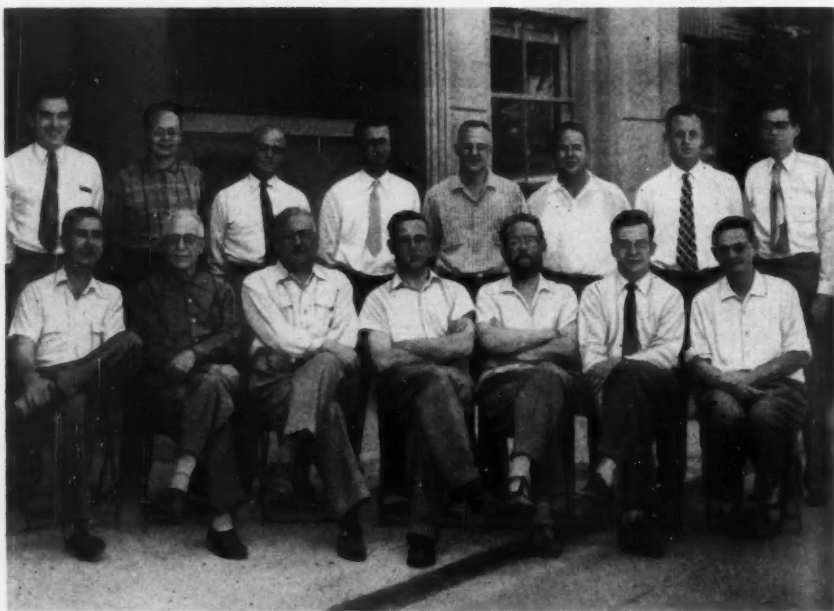
The Station has also conducted investigations on marine mammals. Since 1948 research has been carried out to satisfy Canada's obligations in the Pacific under the International Whaling Agreements, and to learn more about the potential of the stocks on which our whaling industry depends, and how they are related to stocks elsewhere in the Pacific. Canada, Japan, U.S.S.R., and the United States concluded a treaty in 1957 to manage the fur seal herds of the North Pacific so as to obtain the greatest sustained yield possible without damage to other fisheries. Preliminary studies on the food of fur seals were carried out in 1931-32, 1935 and 1952 but, under the new treaty, a more intensive study was commenced in 1958 to determine where they occur and how they affect valuable



The hydraulic model of Hecate Strait completed in 1958 to study the tidal circulation. When the model is filled with water, two gates tilt back and forth under electronic control to produce a replica of tidal rise and fall in all its various phases. Their effects on the circulation are studied by photographing the movement of dyed water.

fish stocks. Sea-lions have been studied to assess the need and develop the means of control to prevent damage to fisheries.

These examples serve to illustrate the growth of the Station's work in the post-war period and how it is related to fisheries problems. There are, of course, many other items in its program, but for these the reader must go to the many publications of the Fisheries Research Board, or visit the Station itself. For general reviews of the work of the Board he is referred to its published *Annual Reports*, and for accounts of special subjects to its *Bulletins*. Both these may be obtained from The Queen's Printer, Ottawa, Canada. Brief notes on the Station's investigations and their results appear in the *Progress Reports of the Pacific Coast Stations* of the Fisheries Research Board, also available from the Queen's Printer. The Nanaimo Station also issues *Circulars* on subjects of special interest to fishermen and the fishing industry. Circulars may be obtained by application to the Station.



Senior scientific staff in 1958. Front row, left to right: J. R. Brett (experimental studies on salmon), R. E. Foerster (salmon), A. W. H. Needler (Director), F. H. C. Taylor (herring), J. D. Strickland (primary productivity), N. P. Fofonoff (physical oceanography), W. E. Ricker (Editor of the Board). Standing: L. Margolis (parasitology), F. C. Withler (Skeena River salmon), F. Neave (high-seas salmon), F. C. Barber (oceanography), W. P. Wickett (stream life of salmon), D. J. Milne (spring and coho salmon), K. S. Ketchen (marine commercial fisheries), J. C. Stevenson (Assistant Director). Absent: J. P. Tully (Oceanographer-in-charge), M. P. Shepard (salmon stock assessments), M. Waldichuk (pollution) and G. C. Pike (marine mammals).

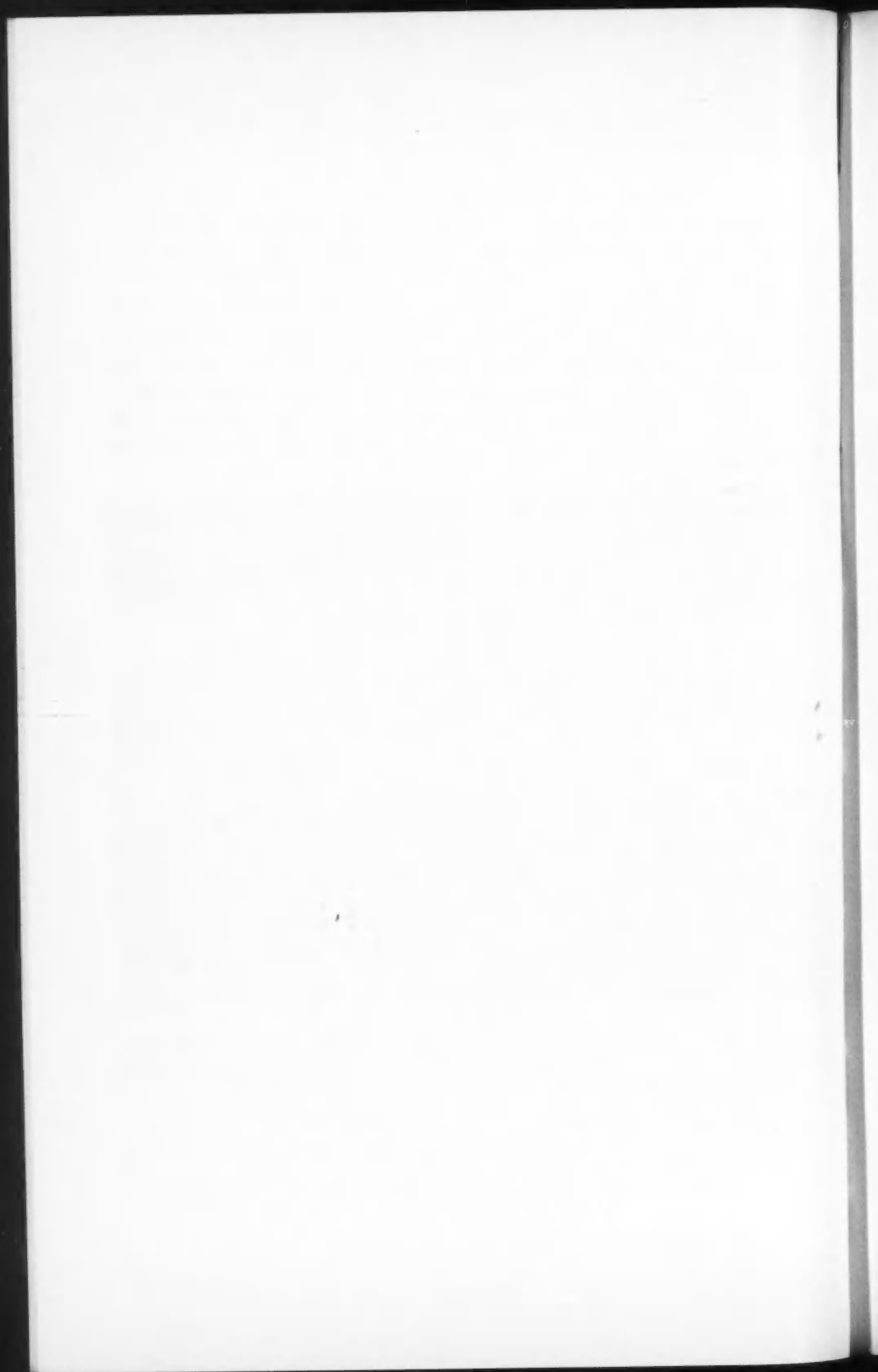
WHAT THE FUTURE HOLDS

True to the original purpose of those who first proposed the establishment of a biological station in Canada at the close of the last century, the Fisheries Research Board of Canada is providing scientific knowledge which is proving to be of great value to fisheries. In its particular field—biological research in the Pacific area—the Board's station at Nanaimo makes a substantial and a growing contribution. The pressing problems of the management of existing fisheries are close to the interests of the fishing industry, and efforts to solve them constitute an important part of the Station's work. Growth of population and industry offer ever-increasing threats to our fish stocks, which have created an urgent demand for research on how to get salmon past obstructions and dispose of wastes with the least possible damage to fisheries. Positive cultural methods of producing salmon and shellfish have unexplored potentials which are being studied and will be the subject of increasing efforts. A large part of the Station's work is required to fulfill Canada's obligations under international fisheries treaties. Less urgent but not less important is the broad exploration of the ocean off our coasts on which to base development of new fisheries and understanding of changes in those we have. Last but not least, all of these activities depend on improving our fundamental knowledge of the life processes of the fish and shellfish, and of the ever-changing climate in which they live.

The growing demand for research on fisheries problems has outstripped even the rapid growth of the Board and the Station in the post-war period. Populations continue to grow and the world's need for food continues to increase, and men must turn more and more to the sea for sustenance. The detailed course of events cannot, of course, be predicted but it is safe to say that the need for research on fisheries problems will continue to grow for some time to come. Sound development is more likely to be limited by resources than by demand, and the most important resource is a body of scientists genuinely interested in the problems, and able to make a broad, thorough and imaginative attack on them.

No field of research offers greater challenges to the scientist or more varied problems to interest him. The unseen world of the ocean cannot be observed directly and is difficult to study, but has secrets of great scientific and economic importance. Every problem of life itself is reflected in fisheries problems; every branch of science must help to solve them. On the Station's staff, physicist, chemist and engineer work with scientists in many branches of biology. The Station's work interests and needs many university scientists.

May the Fisheries Research Board of Canada and its biological Station at Nanaimo long continue to serve the people of Canada in an exciting and profitable adventure of discovery!



Reminiscences of a Director¹

By W. A. CLEMENS

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INTRODUCTION

WHEN I WAS INVITED to contribute an article to this anniversary issue, devoted to some of the events during the period of my Directorship of what was then called the Pacific Biological Station, I hesitated in accepting but it occurred to me that an account of the development of the investigational program of the Station might be of interest to many persons having an interest in marine biology and particularly in fishes and problems of their conservation. Moreover, it seemed that it might provide an opportunity to give recognition to the parts played by many individuals in advancing the work at the Station.

I accepted the appointment as director of the Station with considerable reluctance and trepidation, and only after much persuasion on the part of Dr. A. P. Knight, then Chairman of the Biological Board, Dr. J. P. McMurrich and Dr. A. G. Huntsman. I need not state my reasons for hesitation except that, among other things, I was almost totally ignorant of the fauna of the Pacific coast, especially of the fishes. The reply given to this argument was that a great many of the people in British Columbia were from Ontario and the maritime provinces and from Great Britain, and they did not know the fishes or other animals either. I did find a great lack of knowledge in this respect and this fact resulted eventually in the preparation, in association with Mr. G. V. Wilby, of the bulletin "Fishes of the Pacific Coast of Canada".²

I arrived with my family at Nanaimo on June 1, 1924, aboard the old Canadian Pacific Steamship *Princess Patricia* which docked at the wharf located below the sturdy, stone Federal Building with its clock tower. We were met by Mr. Fred Groth, caretaker of the Station, and loaded with our baggage into his Ford truck. We climbed the steep ramp, turned northward and headed for the Station located on Departure Bay about four miles out of the city. The season had been early and dry and the country side was brown and the roadside grey with dust. The road was narrow and gravelled and so narrow around the Bay that two cars could pass only at a very few turn-out places. The scenery throughout was most attractive—the snug Nanaimo harbour; the quaint town stretching up the hillside, with Mount Benson in the background rising some 3,300 feet; Departure Bay, almost circular in shape with a series of rocky islands in the middle and with steeply wooded shore; a glorious vista out over the blue Strait of Georgia to the snow-capped mountains of the coastal range.

¹Received for publication May 20, 1958.

²Bulletin of the Fisheries Research Board of Canada, No. 68, 1946.

And so after a bumpy, dusty ride we arrived at the Station. There were then three frame buildings on the hillside set amongst tall Douglas fir and strikingly beautiful arbutus trees. The main structure was built in 1908 and consisted of a two-storey portion designed for the director's residence and comprised of a living room, kitchen and bathroom on the main floor and four bedrooms above. Extending out from this part was the laboratory consisting of a long room with work benches along each side and a long table down the middle. Beyond the laboratory was a small library room and an entrance hall. During the preceding winter and spring a basement had been excavated under most of the building and here had been placed the Station's museum, consisting of jars of preserved fishes and invertebrates. Beneath the library was a director's office-laboratory. Also during the winter a small chemical laboratory had been built just beyond the main building. This is still in existence as a coffee-lunch-seminar-room.

To the east of the main building stood a flimsy two-storey structure occupied by the caretaker and his wife, Mr. and Mrs. Groth. Mr. Groth, always called Captain Groth, not only took care of the buildings and grounds but operated the Station boats and used his truck for haulage of supplies and mail. Mrs. Groth provided the meals for the Director and his family and for the investigators.

A wharf some 100 yards in length extended out into the bay and to the float were tied a 30-foot cabin cruiser, the *Ordenez*, a 15-foot open motor boat, the *Snipe*, and a row boat.

This then was the Pacific Biological Station on June 1, 1924, and Captain Groth and I comprised the staff.

At the time of my appointment, I was given no written "terms of reference" but Dr. Knight, Chairman of the Board, had indicated a number of matters to which I should give consideration:

(1) For some years prior to 1924, Dr. Knight had been greatly concerned about the efficiencies of fish hatcheries and so he instructed me to consider the efficiency of the salmon hatcheries in British Columbia and to present a program of investigation to the Board at an early date.

(2) There had occurred a reorganization of the Board involving representation of the fishing industry and a special grant had been made available for the establishment of technological stations at Halifax and Prince Rupert. I was directed to give attention to locating the station at Prince Rupert and organizing a staff.

(3) With the steady expansion of the fisheries, an increasing number of questions had arisen concerning the stocks of fishes and adequate conservation measures for them and my appointment was expected to lead to the development of a program of fishery research and to the acquisition of basic information on the fish and fisheries.

(4) Practically all of the investigations of the Station had been carried on by volunteer summer investigators from the Universities. I was given to understand that I was to make this phase an effective part of the Station's program.

I shall discuss these items in the order in which I had to deal with them.

THE FISHERIES EXPERIMENTAL STATION

The day after I arrived at the Station, Mr. John Dybhavn of Prince Rupert, the Board's representative for the fishing industry on the Pacific coast, and Mr. John McHugh, resident engineer of the Dominion Department of Fisheries at Vancouver, arrived and informed me that I was leaving that evening for Prince Rupert to look over possible sites for the technological station. And so that night I found myself on board the steamer headed for the northern city.

It had been suggested that accommodation for the Station might be obtained in the Trans-Pacific freight shed constructed by the Grand Trunk Pacific Railway. The building was a huge barn-like affair and the expense of fitting up laboratories in one section would have been great. Moreover, it was a very considerable distance from the fish wharves and cold storage plant. Several other possibilities were considered but none was remotely satisfactory. I made a somewhat discouraging report to Dr. Knight who replied that some of the best scientific work had been done in attics and shacks and that it should be possible to find some temporary quarters in which investigational work could be started. During the next several months of search and consideration, it became evident that the most desirable place for the laboratory was on the Provincial Government wharf where large quantities of fish were landed. Negotiations were entered into with the Provincial Government resulting in the construction of a two-storey building, which also provided space for the International Fisheries [Halibut] Commission.

Meanwhile, Dr. C. H. O'Donoghue, a member of the Board, found a young man recently graduated in Chemistry at the University of Manitoba, Mr. D. B. Finn, who was interested in refrigeration problems and in the possibility of an appointment to the Directorship of the Station. In due course the appointment was made. Mr. Finn arranged to secure temporary quarters in the basement of the old unoccupied hotel near the fish cold storage plant. In a short time a laboratory was fitted up, and here Mr. Finn and an assistant, Mr. Roger Reid, commenced their investigations. A couple of rooms were fitted up as living quarters but a plague of rats almost drove the men to distraction. They waged an unceasing battle and were able to endure the situation until the construction of the Station was completed and the move made up-town.

About this time another young chemist was discovered at the University of Manitoba, Mr. H. N. Brocklesby, who was considered for oil research. He was assigned for the summer to the Pacific Biological Station in order to more or less assess his research ability. There was no question as to his capabilities and in due course he took up his duties in Prince Rupert at what was now called the Fisheries Experimental Station. Thus this Station was launched on its career. Thanks to Mr. Dybhavn's untiring interest and support, and to a wise choice of staff, it has had a distinguished record.

A very close association was maintained between the two Stations. Each year, the staff of the Prince Rupert Station came to the Nanaimo Station for most of a week and each member of each staff reviewed his problem and his progress in investigation. I recall how interested the Nanaimo staff was in the ingenious

pieces of apparatus which the members of the Rupert staff devised from alarm clocks, mouse-traps, pieces of car engines, etc.—funds were not plentiful in those days. It occurred to Mr. Finn and me that the stories of the investigations under way at the two stations should be made known to the men of the fishing industry. We recommended to the Board that it issue a series of quarterly Progress Reports. The idea was approved and the series has continued to the present day.

VOLUNTEER INVESTIGATORS

Upon my return to the Nanaimo Station my first concern was the summer volunteer investigators. From the time the Station had been established in 1908, the Board had depended upon University personnel for the conduct of investigations, except for its curators, first the Reverend G. W. Taylor and his successor Dr. C. McLean Fraser. The Board undertook to pay the travelling expenses to and from the Station and to provide board and lodging for those persons accepted as investigators. When I arrived at the Station I found a group of men already at work. These were: Messrs. C. R. Elsey, G. V. Wilby, A. R. Fee, L. L. Bolton—all students from the University of British Columbia, and Mr. G. H. Wailes of Vancouver. A little later Dr. and Mrs. C. H. O'Donoghue of the University of Manitoba and Dr. and Mrs. J. B. Collip of the University of Alberta arrived. These people were all accommodated in tents which were put up around the grounds.

In considering the volunteer investigator situation it was apparent that, aside from the nature of the investigations, there were three things that required attention: first, adequate laboratory equipment and supplies; second, suitable boats for field work and for collecting study materials; third, housing. I realized that all the objectives could not be reached immediately for the appropriation for the Station in 1924–25 was approximately \$14,000. But I was confident that I had a sympathetic Board which would support reasonable presentations. This proved to be the case. I shall recount the progress in the attainment of the above objectives without attention to chronological order.

The laboratory equipment and supplies were very meagre and gradually over the succeeding years I built up a supply of apparatus such as balances, microscopes, ovens, microtomes and many other items and furnished the laboratories with an adequate supply of glassware. A substantial appropriation was allotted each year for the purchase of books and for subscriptions to journals.

I was told before I left the East that the *Ordenez* was reported to be infected with dry rot, that I should have her inspected and, if in bad shape, to sell her and made recommendations for replacement. Captain Groth and I took the boat to Victoria where the Government inspector reported her in need of very extensive repairs. I therefore placed advertisements in the Vancouver, Victoria and Nanaimo papers and presently received a reasonable offer from a man in Victoria. As he signed the purchase papers he remarked that it was quite an honour to buy a boat from His Majesty the King. I was unable to find a suitable boat to replace her with the money available and chartered a pleasure cruiser for the summer. In the fall I decided that the best solution to the problem was to have

the boat builder in Nanaimo, Mr. H. Vollmers, build a 35-foot boat more or less of the trolling type. I entered into an agreement with him whereby he would be paid half the price in one fiscal year and the remainder in the next. I sent the agreement to Mr. J. J. Cowie, Secretary of the Board, in Ottawa and received a telegram stating that I could not commit the Board beyond the present fiscal year and to cancel the agreement. Good old Mr. Vollmers generously agreed to the cancellation and I always retained a warm spot in my heart for him for helping me out of a bad predicament. He had not commenced construction but had purchased some lumber so I reimbursed him for his outlay and presented him with the material. The episode brought the matter of a boat to a head and in due course the Department of Fisheries built a 50-foot boat and turned it over to the Board. It was named the *A. P. Knight*. The vessel was a patrol-boat type, unsuitable for fishing operations, but it did serve the Station well at that stage in its development for collecting materials, for oceanographic work in the Strait of Georgia, and for getting about in the inside waters along the coast. It was equipped with a semi-diesel engine which was without doubt the noisiest on the coast. Its starting was like a cannonade and its putt-putt could be heard for miles.

The *Snipe* was the joke of the Station because of its "tricky" little engine. No one was considered initiated into the Station community until he had rowed it back to the wharf from some expedition.

It seemed to me in the matter of accommodation that the first step should be adequate housing for the Director if he was to live at the Station. I secured plans for a bungalow together with an estimate of the cost and submitted a recommendation to the Board. Approval was given for construction and in a very short time the Director and his family were comfortably provided for. Eventually the living room in the old building became my office and the kitchen became the general office in which was installed a newly appointed secretary-bookkeeper-librarian, Miss Evelyn Keighley.

Then I had installed a furnace and hotwater heating system in the biological and chemical buildings which up to this time had been "warmed" in winter by a fire-place and three stoves.

The next move was to provide living quarters for the volunteer investigators and for newly appointed members of the scientific staff. Again the Board approved my recommendation and presently a large dormitory was built. It was called the Residence Building and included a large kitchen and two associated rooms, two dining rooms, a large lounge and a very considerable number of bedrooms.

With the acquisition of boats and buildings it was necessary to add to the non-technical staff and so Mr. and Mrs. Thomas Russell—Tommy and Winnie—came to the Station and served so loyally throughout the years. As the Station's scientific program expanded, Miss Ethel Robinson was appointed as Secretary.

And here I wish to pay tribute to the contribution which my wife, Dr. Lucy Wright Smith, made to the functioning of the Station. She undertook the task of planning and supervising the furnishing of the Residence Building and then the

responsibility for its operation including the organization and supervision of the staff. From the time of our arrival she assumed responsibility for all matters pertaining to the social welfare of the volunteer investigators, who in many cases were accompanied by their wives and children, and was the gracious hostess to the very many visitors to the Station. She took a keen interest in the research work and during the winters worked with me on the annual sockeye salmon report for the Provincial Fisheries Department.

I am satisfied that I organized the volunteer worker system so that it made a real contribution to the Board's work. True, there were some disappointments in the research efforts, but with a few exceptions the investigators applied themselves steadily and faithfully to their problems not only during the summer months but after their return to the Universities. Eventually they submitted detailed reports, the majority of which were subsequently published in Contributions to Canadian Biology or in other journals. Because of the limited time and the season, the amount which they contributed directly to fisheries research was limited but they did advance the knowledge of the systematics and life-histories of the marine plants, invertebrates (especially shellfish), fishes, and oceanography, and all was accomplished with a relatively small monetary outlay on the part of the Board.

The depression of the early 1930's with its severe curtailment of funds brought the volunteer investigator arrangement to an end in 1934. That this or some similar system was not re-instated seems to me unfortunate, because the association of University and Station personnel was mutually stimulating and beneficial. In recent years some faculty members and many students have been employed in fisheries projects but it has been the systematic and ecological work with the invertebrates which has been neglected and it is such work that University personnel can well carry out. Because of lack of funds, the University of British Columbia has not been able to establish a biological station and so for twenty years little has been done in this field—except for the studies on polychaete worms carried out so steadily and enthusiastically by Mr. and Mrs. C. J. Berkeley as volunteer investigators at the Station. However, the Board became increasingly involved in an expanding program of fisheries investigations and decided to direct practically all its energies and resources in that direction.

FISHERIES INVESTIGATIONS

It was abundantly evident that there was pressing need for concentrated investigations of the fishes to keep pace with the developments in the fisheries. Dr. C. McLean Fraser had contributed some basic information concerning herring and salmon, Dr. A. Willey on halibut, Dr. C. H. Gilbert on sockeye salmon, Dr. W. F. Thompson on herring and halibut, and Dr. J. Stafford on the native oyster. The investigations of the last three mentioned men were supported by the Provincial Fisheries Department.

Very shortly after my arrival on the coast agreement was reached between the United States and Canada on the formation of the International Fisheries

Commission—now the International Pacific Halibut Commission—and it was hoped that international agreement might be reached in regard to the sockeye salmon of the Fraser River.

The following account of some of the fisheries investigations includes the story of the study of hatchery efficiency at Cultus Lake.

HATCHERY EFFICIENCY

While still at the University of Toronto, I received a letter from a graduate student at the University of British Columbia, Mr. R. E. Foerster, enquiring if he might be accepted as a candidate for the degree of Doctor of Philosophy. I took the letter with the enclosed credentials to Dr. B. A. Bensley, Head of the Department of Zoology, who approved of the application. And so toward the end of the summer of 1923 the young westerner arrived with his bride. His doctoral research was on the limnological conditions in Cultus Lake in relation to the production of sockeye salmon. He completed the requirements for the doctorate in the spring of the year in which I accepted the position of Director of the Station. When Dr. Knight specified an investigation of the efficiencies of the salmon hatcheries I recommended the appointment of Dr. Foerster to the Station staff to take part in this project. The appointment was made.

Dr. Foerster arrived in Vancouver during the summer and I instructed him to locate at Cultus Lake, to continue his studies of sockeye salmon production and to prepare a program for the investigation of salmon hatcheries. Dr. and Mrs. Foerster were able to obtain a house-boat for accommodation. This had been built by Mr. Hubert Evans, the popular writer, who for a number of years was superintendent of the Cultus Lake hatchery. At that time there were no cottages around the lake as the area was under a timber lease. Presently, a block of land at the north end of the lake was sold to a newly formed organization known as the Cultus Lake Park Board. When the program to be described later was adopted the Biological Board obtained two lots on the water front and built a cottage and a laboratory.

After the departure of the summer people in 1924 I arranged for the formation of a Fishery Advisory Committee consisting of Major J. A. Motherwell, Chief Supervisor of Fisheries; Mr. J. P. Babcock, Assistant to the Commissioner of Fisheries, Victoria; Dr. A. H. Hutchinson and Mr. John Dybhavn, members of the Fisheries Research Board; Dr. C. McLean Fraser; and Dr. C. H. O'Donoghue. In the meantime Dr. Foerster worked assiduously on an outline of a program of hatchery investigation. After a number of conferences with him I arranged a meeting of the above Committee to which Dr. Foerster presented a brief on a proposed program. It recommended that a direct attack be made on the problem by actually counting each year the number of seaward-going yearling sockeye resulting from the actual number of adult females present 18 months previously. The comparison of the relative efficiencies of natural reproduction and the fish cultural methods of fry and egg planting were to be based upon the number of eggs involved in each procedure.

It was recommended that Cultus Lake be the site of the study because (1) a hatchery was located there; (2) it was a small lake with a relatively small salmon population; (3) it was not subject to flood conditions and was free of ice throughout the winter; (4) the necessary weirs could be readily installed in the outlet stream and operated without difficulty; (5) it was readily accessible; (6) a considerable amount of information was already available concerning the salmon population and the limnological conditions; (7) no other lake in the Fraser River system appeared to offer facilities at all comparable with those at Cultus Lake. It was proposed that the investigation be carried out over a period of at least 9 and possibly 12 years so as to test each method of propagation at least three times. A wooden picket weir was already in place in the outlet of the lake and it was proposed that a weir for intercepting the yearling fish be installed consisting of a series of panels of coarse wire screening in duplicate so that one set could be raised for cleaning at any time and all removed after the migration period. The weir would be placed slightly diagonally across the stream so as to lead the young fish into pens where they could be enumerated and then released downstream. It was recommended that the Department of Fisheries assign its most capable and experienced fish cultural officer to the Cultus Lake hatchery and that Dr. Foerster be given a non-scientific assistant.

I believe that the members of the Committee were somewhat overwhelmed with the novelty and magnitude of the proposal but after a lengthy and critical discussion, they unanimously endorsed it and recommended it to the Board. As I recall, the reactions of the Board members were much the same as those of the Committee members but the investigation was authorized. No time was lost in getting the program under way. Mr. Alex Robertson was chosen by the Department of Fisheries as Superintendent of the hatchery and Mr. W. F. Baxter was engaged to help Dr. Foerster. Some years later Mr. W. E. Ricker was appointed to the Station staff and assigned as scientific assistant to Dr. Foerster. The basic program proceeded according to schedule and when three tests of each of two methods of propagation and two tests of the third had been made the Board decided to bring this phase of the investigation to an end since no significant differences appeared among the methods—each showed approximately a 3 per cent production of yearlings on the basis of the number of eggs available. The following statement was adopted by the Board and in view of this the Department of Fisheries closed all the salmon hatcheries in British Columbia: "On the basis, therefore, of the above results, it may be concluded that in an area such as Cultus Lake, where a natural run of sockeye occurs with a reasonable expectancy of successful spawning, artificial propagation for purposes of continuing the run to that area is unnecessary, and, if producing any additional results over natural spawning, these would not appear to be in any way commensurate with the cost".

This investigation was an original method for the study of fish production and will always remain as a classic. It is greatly to Dr. Foerster's credit that through his vision, careful planning and careful attention to details, the project was carried through without any change in or disruption of the basic program.

To me and, I believe, to many persons a most startling fact revealed by the study was the high mortality occurring during the period from egg deposition to seaward migration. From some general observations, it appeared that predation on the part of other fishes might be responsible for a great deal of the losses. The Board approved of a concentrated effort to reduce the number of predators and competitors in the lake and determine if the numbers of out-going yearling sockeye were thereby increased. A substantial increase in numbers of young migrants was demonstrated. During the years of the investigation knowledge of the biology of the sockeye was advanced in many respects. With the formation of the International Pacific Salmon Commission, the Board's program of investigation at Cultus Lake was terminated.

SALMON MIGRATION

In the autumn of 1924 I was invited by Major Motherwell, Chief Supervisor of Fisheries for British Columbia, to attend a conference in Seattle for the consideration of some salmon problems of international concern. A considerable number of persons were in attendance among whom were: Major J. A. Motherwell, Mr. J. P. Babcock, Mr. Henry O'Malley, Mr. Miller Freeman, Mr. M. Hoy, Dr. C. H. Gilbert, and Dr. W. H. Rich. Very considerable discussion took place on the ocean fishing for spring salmon and it was agreed that it would be most desirable for Canada and the State of Washington to carry out tagging programs to obtain information on the movements, migration and life-history of this species. The conference also agreed that it was desirable to provide for a series of future meetings and so formed an organization under the imposing title "The International Pacific Salmon Investigation Federation". Upon my return to the Station I considered carefully with Major Motherwell the possibility of tagging salmon off the west coast of Vancouver Island. Together we prepared a detailed and extensive program with estimates of costs. This, I believe was submitted to the Advisory Committee and approved and subsequently by the Department of Fisheries and the Board. The Committee also recommended the appointment of an investigator to the staff of the Station who would undertake sea investigations of salmon. The Board acted quickly in this matter and on the recommendation of Professor E. E. Prince, appointed Dr. H. C. Williamson, formerly of the Fishery Board for Scotland. This wiry bearded Scotsman arrived on the coast in the spring of 1925, and was given charge of the salmon tagging program.

Arrangements were made with experienced troll fishermen having good-sized, sea-worthy boats to take taggers aboard. As each fish was caught and brought to the boat its weight was estimated by the fisherman and tagger, and it was tagged and released as quickly as possible. The weights were recorded and later payment was made on the basis of weight at the current prices. The program called for (1) tagging spring salmon off Barclay Sound, Vancouver Island, with headquarters at Ucluelet, and off the Queen Charlotte Islands at Hippa Island; and (2) tagging sockeye salmon at the traps on Haystack Island off Portland Inlet and from purse-seines in Deepwater Bay on the east coast of Vancouver Island.

Dr. Williamson was assigned two students from the University of British Columbia (Messrs. F. H. Bell and A. Fee) and three hatchery officers as assistants. Details of the operations need not be given here but over 2500 fish were tagged. A reward of 50¢ was offered for the return of each tag and by the end of that year 343 were sent in, representing 13 per cent recovery. The results of the spring salmon tagging off Barkley Sound showed a southeast movement, with 60 per cent of the returns from the Columbia River. Surprisingly, two tags were returned from the Sacramento River in California. The returns from the Queen Charlotte Island tagging were likewise from the southeast as far as Marshfield, Oregon. At the second meeting of the Federation I was able to report a real contribution to the knowledge of salmon movements along the Pacific coast. Unfortunately, the American agencies to the south were unable to carry out any work, partly, it was said, because of refusal of co-operation on the part of the fishermen. The results of the 1925 tagging program were so interesting and valuable that further programs were undertaken in subsequent years. A goodly number of university students were employed—among them Messrs. C. McC. Mottley, J. L. McHugh, L. L. Bolton, H. J. Alexander, M. MacPhail, D. Beall and J. L. Kask, the present Chairman of the Fisheries Research Board.

I was convinced that it was necessary to understand the functioning of the salmon's sense organs in order to understand at least in part, the migrations of both adults and young. Dr. E. H. Craigie of the University of Toronto came to the Station as a volunteer investigator in 1925 and I discussed with him the possibility of carrying out a study of the relation of the olfactory organs of adult salmon to their ability to find their way to the spawning stream. Dr. Craigie carried out some experiments in cutting the olfactory tracts of fish and decided it would be feasible to do the operation quickly and satisfactorily on commercially caught sockeye salmon. He accompanied the tagging crew to Deepwater Bay and there cut the olfactory tracts of 259 salmon. These were tagged as well as 254 "normal" sockeye. Of these, 28 "operated" and 62 normals" were subsequently caught in the Fraser River and 2 "operated" were taken far from the Fraser River. Aside from whatever conclusions may be drawn from these results, the experiment was of interest in indicating possible future experimental work. Unfortunately, for several reasons, this line of endeavour was not continued, nor were other researches on sense organs. I had hoped to convert the basement museum room into an experimental laboratory but the freshwater supply at the Station was very limited. Even had it been adequate, recirculation systems with filters would have had to be installed and the costs would have been considerable. But over and above all this there appeared to be a lack of men in Canada who were interested in and trained for this kind of research, and it was not until such men as Drs. K. C. Fisher and F. E. J. Fry at the University of Toronto developed the field of experimental zoology that young men became available for such researches.

PINK SALMON

In 1930 another major salmon investigation was undertaken. Large runs of pink salmon enter Massett Inlet of the Queen Charlotte Islands, whence they

proceed to several splendid spawning streams tributary to the inlet. But the runs occur only in even-numbered years. Since the pink salmon matures invariably at two years of age there can be no overlapping or inter-breeding between fish of the alternate years, hence the population of the alternate years are absolutely distinct from one another. Thus one population cannot contribute to the other and one may decline and disappear as has apparently been the case in Massett Inlet. There were two canneries on the entrance to the Inlet and these could operate only every other year. It was natural therefore that the operators should request an investigation of the possibility of establishing a pink salmon run in the "off" year. The Board approved of an investigation which would (1) add to the knowledge of the biology of the pink salmon, (2) discover the factors involved in the lack of salmon in the "off" years, (3) include an experiment in transplantation to determine quickly the possibility of establishing a run in the "off" year. Dr. A. L. Pritchard was appointed to the staff for the project and later Mr. W. M. Cameron was appointed as assistant.

McClinton Creek was chosen for the work and a field station was established there which included "bunk" houses and a small hatchery. A weir was built across the stream with removable panels of wooden pickets and wire screening so that adults migrating upstream and fry moving downstream could be enumerated. This portion of the program to determine the productivity of pink salmon in terms of fry and the causes of mortalities in egg, alevin and fry stages was carried out over a period of years. The results of the six determinations showed an average fry production of 10 per cent with a range from 7 to 24 per cent. There was thus a very high mortality largely due to climatic and biological factors including predation by trout.

The transplantation experiment was carried out in the "off" years. Eggs were obtained from the Tlell River on the east coast of Graham Island and transferred to the hatchery at McClinton Creek, the number ranging from approximately 700,000 to 1,130,000. In 1931 and 1935, approximately 878,000 and 506,000 fry respectively were liberated, considerable numbers of which were marked by the removal of fins so that positive proof of return of adults might be obtained. In 1933, 540,000 eyed eggs were planted in the gravel beds of McClinton Creek. A month later an unprecedented freshet occurred and washed out all the spawning beds. Only five fry appeared at the weir the following spring. From the 1931 experiment no marked fish appeared in McClinton Creek or in any stream tributary to Massett Inlet or in Tlell River but forty were taken in the vicinity of the Fraser River. One unmarked fish appeared in McClinton Creek. From the 1935 experiment four marked two unmarked fish came into McClinton Creek and no marked fish were discovered or reported in any other area. The three attempts to establish runs of pink salmon in the "off" years in McClinton Creek were thus failures. Unfortunately this part of the investigation did not provide an explanation of the "off-year" phenomenon. Many important features of the biology of the pink salmon were obtained but need not be discussed here. Requests for a sockeye salmon investigation on the Skeena River were largely responsible for the cessation of the McClinton Creek project.

PILCHARD AND HERRING INVESTIGATIONS

While the salmon, because of their great economic importance, were receiving particular attention, other fish and fisheries were demanding study. Prior to 1925, relatively small quantities of pilchards were caught during July, August and September in the inlets of the west coast of Vancouver Island for canning and reduction to oil and meal. In due course the fishery for reduction purposes was intensified so that the catch was increased more than ten fold. More reduction plants were built until some fifteen were in operation, fishing was extended from the inlets to the off-shore waters and the annual catch of pilchards reached a peak of slightly over 75,000 tons. Naturally the Dominion and Provincial Fisheries Departments as well as the operators and fishermen were deeply concerned as to the size of the stock of pilchards and the possibility of over-exploitation. The fish were present off the west coast of Vancouver Island during the summer and disappeared in the fall, so that there was much speculation as to whether they constituted a population which moved off shore in the autumn or were a part of a large population occurring off California. So it came about that the Board was requested to undertake an investigation. Dr. J. L. Hart was appointed to the staff to organize the investigations. He was assisted by Messrs. W. R. Whitaker, D. Beale, H. B. Marshall and others. The Provincial Fisheries Department undertook to make an annual grant to further the project. Two lines of endeavour were taken up immediately, the first was the setting up of a sampling-statistical system whereby the character of the catch and the intensity of the fishery could be determined annually. The second was to find out if the pilchards appearing off Vancouver Island were a part of the California population. Two lines of attack were followed in this problem. The first consisted of a very critical examination of fish caught in the two areas. The results showed no morphological differences, but the Canadian-caught fish were largely upper-age individuals. The second was a direct attack in which Canadian and Californian investigators undertook a co-operative tagging program using internal tags. These consisted of small metal plates on which were stamped numbers and letters to indicate the area of origin. The tags were inserted in the abdominal cavities of the fish and recovered from the meal line in the reduction plants by the use of strong electro-magnets. Following extensive tagging programs in California and British Columbia waters, Canadian-inserted tags appeared in California reduction plants and California tags in Canadian plants. From all this it was evident that the Canadian fishery was based upon what might be called the California population of pilchards, since the main body was evidently to the south where the annual United States catch was over 500,000 tons. The logical conclusion was that the fish appearing in Canadian waters were an overflow of larger, older individuals of the California population. It was also evident that the Canadian fishing effort with an annual catch up to 75,000 tons could not be a significant factor in the decline of the pilchard stock or in the eventual disappearance of the pilchards from British Columbia waters.

As fewer and fewer pilchards came northward more and more reduction plants closed down. The operators of the surviving plants considered the possi-

bility of using other kinds of fish for the production of oil and meal, and naturally turned to the herring. However, the Provincial Government opposed unrestricted use of herring for reduction on the grounds that this fish should be used for human consumption and that an intensive fishery such as had developed for pilchards might quickly deplete the stock. The Dominion Department of Fisheries took the stand that the herring should be used in the most economical manner and that its primary concern was to insure the maintenance of stock. The operators stated that the supply of herring was far beyond what could be marketed in the salted, canned and smoked forms under the existing market conditions. The Provincial Government held the key to the situation because it could refuse to issue licences for the operation of reduction plants. Finally a compromise was reached, about 1935, wherein the Provincial authorities agreed to widespread reduction of herring on condition that an immediate intensified investigation be undertaken to determine the extent of the herring population, and the extent to which it might be used without depleting the stock. The Provincial Fisheries Department undertook to contribute annually toward the cost of the investigation. Dr. Hart organized the program and Dr. A. L. Tester shared the responsibility for the work. Messrs. D. C. G. MacKay, R. V. Boughton, J. L. McHugh and a number of technicians assisted with the work. Fortunately, an investigation of the herring had been under way for a number of years and had included the establishment of a sampling-statistical system. The enlarged program included an extensive tagging project. The latter was important because, in the consideration of any effective fishery regulations, it would be necessary to know whether the herring moved freely up and down the coast and thus consisted of one large population, or whether they occurred as a series of more or less discrete units and hence regulations might need to vary from area to area. For the recovery of the tags, electronic tag detectors were brought into use. The apparatus had been developed by a group of investigators at the University of Washington. Briefly, it consisted of an electric field maintained in balance within a coil placed around the conveyor carrying the herring into the reduction plant. When a herring containing a tag entered the field a disturbance was set up which was carried to an apparatus which in turn sent an impulse to a mechanism which opened, for a brief period, a trap door in the chute just beyond the coil. A number of herring dropped into a bin, including the one containing the tag. Later the investigator had to sort out the tag-bearing herring from the lot precipitated into the bin. The results of the tagging work have shown that the herring do occur in a series of more or less distinct populations along the coast.

Many other studies of the herring have been carried out so that a very large body of information has been obtained which has given a sound basis for regulatory measures. Assurance has been provided that the stocks of herring are not being depleted and reduction operations have continued to the present day.

TROUT

When I came to the Station, the Dominion Department of Fisheries had the responsibility for the conservation of the trout in British Columbia waters and

had carried out various fish-cultural practices including the operation of several hatcheries. Questions concerning the relationships among the trout and fluctuations in abundance in various lakes were constantly being asked, so I invited Professor J. R. Dymond of the University of Toronto to spend a summer in a survey of the situation. He accepted and I provided him with an assistant, Mr. C. McC. Mottley. The results were presented in a report which was later issued in booklet form: "The Trout and other Game Fishes of British Columbia". Following this, Mr. Mottley was appointed to the staff. One of his early projects was the rearing of young trout at the Nelson hatchery under constant and differing temperatures, demonstrating that the number of scales along the side of the body was correlated with the temperature of the water during the early development period. Since heretofore scale number had been largely relied upon to distinguish Kamloops trout from the steelhead, the results led to the acceptance of the idea that the Kamloops trout is a non-sea-going form of the steelhead. Mottley then commenced a study of the population of Kamloops trout in Paul Lake, where the stock appeared to be at a very low point. No other species of fish lived in the lake at this time and this fact, together with such circumstances as the presence of a fishing lodge, a single access road, a fairly good history of the fishing on the lake, and a fish cultural establishment at the upper end, all combined to make a situation favourable for the investigation. It was soon discovered that reproduction was at a very low level. Over a period of years, precipitation had been scanty and the inlet stream had been ineffective for natural spawning or for hatching out "planted" eggs. A program of fry liberation in the lake was instituted with success. Dr. D. S. Rawson of the University of Saskatchewan assisted in the program during one summer by making a limnological study of the lake. He also carried out surveys of a considerable number of lakes in the southern interior of the Province. Some time later, Dr. Rawson, Mr. J. L. McHugh and I carried out an extensive investigation of Okanagan Lake. All these surveys provided much basic information concerning the limnological conditions existing in many of the important trout lakes in the middle section of the Province.

When the salmon hatcheries were closed, the Department of Fisheries turned over the Cowichan Lake hatchery to the Board for experimental purposes. Dr. Mottley instituted a program of study on the introduction of Atlantic salmon and brown trout and the use of ponds in the culture of these species and of rainbow trout. Investigations were also conducted on spring and coho salmon. Dr. G. C. Carl was appointed to the staff to assist in this work. Upon the resignation of Dr. Mottley, Mr. Ferris Neave, of the University of Manitoba, replaced him.

Originally, the water supply for the ponds at the hatchery had been obtained from a small stream but this was inadequate in mid-summer. So a pumping system was installed whereby water was pumped from the Cowichan River. During the first summer in which the system was in effect, it seemed that all the pathogenic species of bacteria and protozoa of the Cowichan River accumulated in the ponds and infected the fish so that the stock was almost a total loss. Various

methods were considered for meeting the situation and finally the decision was made to build a sand filter and to re-circulate the water. The system proved to be successful, but shortly after this the program was discontinued—perhaps to the great relief of the investigators, who were under constant strain by reason of the numerous failures of the diesel engine.

Some time during this period a very heavy mortality of whitefish occurred in the Elk River near Fernie. Dr. D. C. B. Duff of the University of British Columbia was asked to investigate. Examination of the fish disclosed for the first time the presence of the fish disease furunculosis in British Columbia. Then followed an outbreak of the same disease among the cutthroat trout at the Cranbrook hatchery. In the course of his investigations, Dr. Duff discovered that a considerable percentage of the fish used in the egg collection operations were carriers of the disease as shown by cultures from the kidneys. Treatment of the eggs with acriflavine was instituted at the hatchery, which was placed under quarantine so that no eggs were shipped outside the area. Dr. Duff continued researches on the furunculosis organism for some years, and developed a vaccine which could be incorporated in the food.

SHELLFISH

Around 1924 and 1925 considerable interest was aroused on the coast by reports that some Japanese fishermen had introduced a Japanese oyster into British Columbia waters with some success. Mr. C. R. Elsey, as a volunteer investigator at the Station in 1924, undertook a study of the situation. He continued the investigations for several summers and then was appointed to the staff. He had as assistants from time to time Messrs. G. C. Carl, E. C. Black, H. Fasmer and others. The culture of the Japanese oyster increased rapidly and this species soon became dominant commercially. The detailed basic knowledge of the biology of the three species of oysters (Native, Japanese and Atlantic) in British Columbia waters and of their economics resulted from Dr. Elsey's endeavours. When he resigned to join the staff of British Columbia Packers, Mr. Ferris Neave carried on the work temporarily and then was succeeded by Mr. D. B. Quayle.

Investigations of commercial clams were initiated by Dr. C. McLean Fraser assisted by Mr. J. L. Kask and Miss Gertrude Smith who, as volunteer investigators, made extensive studies of the life histories. Subsequently Messrs. Neave and Quayle extended the work into the fields of population dynamics and economic harvesting.

A survey of commercial crab fishing was made by Mr. D. C. G. MacKay, who followed this up with an intensive research on the development and growth of the species.

The systematics and life histories of the prawns (mostly called shrimps on the local market) of British Columbia waters were studied by Miss Alfreda Berkeley.

Under the heading of shellfish, reference may be made to the pile- or ship-borer or "teredo". Dr. F. D. White of the University of Manitoba, as a volunteer

investigator, commenced the program of studies which was later extended by Messrs. Elsey and Black to a survey of the incidence of the borers along the coast in relation to ecological conditions.

OCEANOGRAPHY

I have included oceanography under the major section of Fisheries Investigations because a real knowledge of the physicochemical environment is essential for an understanding of the fisheries. Being trained as a limnologist, I was rather surprised on coming to the Station to find how little was known of the physicochemical conditions of the sea along the British Columbia coast. Dr. C. McLean Fraser, my predecessor, had instituted a daily record of temperatures and salinities at the Station wharf and also at the Quarantine Station at William Head through the generous cooperation of Mr. I. E. Cornwall. Dr. A. T. Cameron and Dr. Fraser had published some records of temperatures and salinities obtained in connection with a kelp survey. I was confident that the Board would approve of a sound program but I was so fully occupied with other matters that I postponed action.

Then Dr. A. H. Hutchinson of the University of British Columbia undertook what he termed a bio-hydrographic study of the Strait of Georgia. This extended over a number of summers and several university students participated, including Messrs. R. H. Fleming, C. C. Lucas, Murchie MacPhail, E. C. Black and Miss Mildred Campbell. The investigation indicated many of the correlations between the physicochemical conditions in the Strait of Georgia and the production of phytoplankton. In summer the upper water of the Strait because of its stability attains temperatures of 20° or even 22° Centigrade, and because of the inflow of freshwater from the Fraser River it has a relatively low salinity. In contrast, the upper water on the west coast of Vancouver Island, because of turbulence and the "upwelling" of deep water, has low temperatures of 12° to 15° Centigrade and a relatively high salinity. Thus the flora and fauna of the Strait of Georgia differ in many respects from those on the west coast of Vancouver Island. But above the scientific results, the investigation served to attract attention to oceanography and also helped me to organize ideas.

A most important consideration was that of the appointment of an oceanographer. I had maintained a fairly close association with the members of the staff of the Friday Harbor Biological Station of the University of Washington and had discussed oceanographic matters at various times with Dr. T. G. Thompson. It was natural therefore that I should ask Dr. Thompson if he would be interested in joining our staff and developing an oceanographic program off the British Columbia coast. He indicated a decided interest but said he did not wish to make a commitment immediately. One Sunday afternoon some time later, a large yacht, the *Blue Peter*, came into Departure Bay and tied up at our wharf. On board was a group of men including Mr. Miller Freeman (the owner of the vessel, I believe); President L. M. Spencer of the University of Washington; two or more Deans and several other members of the university's staff, including Drs. Thompson, Guberlet, Miller and Utterback; Dr. Frank Lillie of the

University of Chicago; and Mr. Max Mason of the Rockefeller Foundation. After greetings and a tour of the Station we assembled in the Residence building for afternoon tea. Presently Dr. Thompson took me aside and said that there was a good possibility of the Rockefeller Foundation providing a substantial endowment for the development of oceanography at the University of Washington and if this came about he would be rather under obligation to contribute to the organization. The endowment materialized and Dr. Thompson became the Director of their Oceanographic Laboratories.

I then turned my search to Canada and learned of a young chemist, graduate of the University of British Columbia, then completing a year of post-doctoral study in Germany. Thus it came about that Dr. N. M. Carter became our chemist and oceanographer. He collaborated with Dr. Hutchinson and commenced an investigation of some of the inlets of the coast. About this time a number of pollution problems came up. Further, the Station was asked to carry out a series of analyses of salmon, lingcod and oysters in relation to food values and to obtain some basic data on the salting of herring. The amount of work was so great that an assistant became essential and Mr. J. P. Tully, a recent graduate in chemistry at the University of Manitoba was appointed. Mr. Tully came to the Station with a burst of boisterous enthusiasm which seemed a combined product of the prairie environment and Irish ancestry and which added a "sparkle" to the Station group. When Dr. Carter was transferred to the directorship of the Prince Rupert Station in 1933, Mr. Tully became the oceanographer and proceeded almost single-handed without adequate funds or vessels, to develop the field of dynamic oceanography.

Investigations in the Strait of Georgia were continued and in addition some synoptic surveys were made on the west coast of Vancouver Island. These were made possible through the much appreciated co-operation of Mr. H. D. Parizeau, Chief Hydrographer in British Columbia, in providing accommodation on the survey vessel the *Wm. J. Stewart*, and of the Royal Canadian Navy in supplying H.M.C.S. *Armentières* under Commander H. W. S. Soulsby. Arrangements were made for a number of lighthouse keepers along the coast to take daily sea water temperatures and water samples.

Correlations between ocean conditions and the fish and fisheries require a considerable accumulation of data, usually over an extended period of time. This has been particularly true on the British Columbia coast because of the extensive and varied nature of the ocean conditions and lack of knowledge of the fishes themselves. So, while progress appeared to be rather slow in what may be termed fisheries oceanography, objectives were clarified and sound foundations laid for future advances.

A significant investigation was that of Alberni Canal. A company desired to construct a pulp mill at Port Alberni and asked the Department of Fisheries for instructions regarding the liberation of the effluent into Alberni Canal. The Department of Fisheries asked the Board to investigate and the problem was assigned to Mr. Tully. Mr. Henry Vollmers, with his large new trolling boat, was engaged for the project. The fish hold was fitted up for a laboratory, and on this

boat Tully and Vollmers lived and worked. At a later stage the *A.P. Knight* was used. After accumulating and analyzing a mass of data, Mr. Tully decided he needed a model of the upper end of the Canal in order to interpret and confirm his conclusions as to the water movements. With the assistance of three young lads, R. L. I. Fjarlie, H. J. Hollister and W. Anderson, and with plaster of Paris, buckets, pulleys, hoses, an electric fan and parts of alarm clocks, there appeared a model approximately 6 by 4 feet complete with tides, river flow and winds, all recorded by well-devised gauges. I was intrigued by all this activity and eventually found myself perched on a stool on a table, looking down on the model and recording on a diagram the flow of a dye introduced to represent the pulp mill effluent. Needless to say, I was replaced by a camera. So the model idea was introduced at the Station. Later a larger and more effective model was built on the hill above the Station but the little model in the Chemistry building will always remain as a symbol of vision and ingenuity.

I have attempted to give a reasonably connected account of some of the events which occurred during the period of my dictatorship of Pacific Biological Station. As indicated, I gathered together for the staff a nucleus of young, enthusiastic men who formed a congenial and mutually stimulating group. Each person was given his problem or problems and thrown largely on his responsibility. I acted as consultant, "hormone" and co-ordinator. The men responded admirably and subsequently all went on to positions of trust and high responsibility and achieved high accomplishments. To them I am deeply indebted not only for their scientific contributions as members of the Station staff but also for their co-operation and loyalty at all times. To them, to the volunteer investigators, to interested members of the Fisheries Research Board, and to all others who contributed to the advancement of the Station's program I am truly grateful.

A Note on the Response of Developing Chum Salmon Eggs to Free Carbon Dioxide in Solution¹

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PROCEDURE AND RESULTS

WHILE CARRYING OUT a study of the effects of low oxygen on the eggs of chum salmon (*Oncorhynchus keta*) (Alderdice, Wickett and Brett, 1958), the question arose as to the response of eggs to free carbon dioxide at low dissolved oxygen concentrations. Where water perfuses an egg mass slowly, the extraction of oxygen for respiration will remove a considerable proportion of the available supply. Concurrently there will be a build-up in the concentration of metabolic waste products in the water, including carbon dioxide.

To examine this experimentally, a series of four bottles, each with a volume of approximately 600 ml., was set up to contain various concentrations of carbon dioxide in solution, all at a concentration of 2.5 ppm. dissolved oxygen. Samples of 50 eggs were inserted into each bottle. The bottles were sealed from the atmosphere by a mineral oil plug. The water content of the bottles was circulated gently by means of straight glass stirring rods projecting through the oil seal and controlled by variable-speed electric motors. The eggs were allowed to respire for nine days in the closed containers.

On completion of the experiment the eggs were left in the bottles and a flow of normal water was introduced. It was considered inadvisable to handle the eggs at that time because of their extreme sensitivity to mechanical shock in an early state of development. The eggs were subsequently transferred to trays on the thirty-fourth day of incubation in order to follow effects of the experimental conditions up to the time of hatching.

Eggs used in the tests were stripped from mature salmon at Cook Creek, B.C., and were incubated for 14 days at an average temperature of 7.7°C., equivalent to a summed thermal history of 107.8 Centigrade degree-days, prior to experimentation. Tests were carried out at 10°C. Levels of oxygen and carbon dioxide were determined by titration in each of the four experimental bottles before and after the period of exposure. The water supply in which the eggs were incubated contained about 1.5 ppm. free carbon dioxide at a pH of 7.5 and total hardness equivalent to 20-22 ppm. as CaCO₃. Data obtained from the tests are presented in Table I.

Following exposure to the experimental conditions and prior to their removal to incubation trays, the eggs in bottles Nos. 2 and 4 were subjected to accidental cessation of water flow on two occasions for periods of 12 hours or less through the formation of air-locks in the inlet lines. Only on the first occasion, in bottle 2, was the air-lock followed by a small increase in mortality for a short period.

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TABLE I. The effect of various concentrations of carbon dioxide at a low level of dissolved oxygen on the ability of early incubation stage chum salmon eggs to utilize dissolved oxygen. Fifty eggs were used at each level. Experimental temperature, 10°C. Length of time eggs allowed to respire in the closed bottles, 9 days.

	Bottle:	1	2	3	4
Dissolved oxygen, ppm., at start		2.53	2.52	2.50	2.53
Dissolved carbon dioxide, ppm., at start		6.5	124	203	243
Dissolved oxygen, ppm., at completion		0.17	0.08	1.38	2.26
Dissolved carbon dioxide, ppm., at completion		15	115	161	159
Dissolved oxygen utilized, ppm.		2.36	2.44	1.12	0.27
Number of eggs hatching successfully		43	7	1	0

Although this experience might merely have accelerated somewhat the coagulation of eggs which would have died eventually as a result of the experimental exposure, the information obtained on the resulting live hatch in each of the two affected samples is suspect.

The effect of carbon dioxide on oxygen utilization by the eggs and the recorded live hatch at each level are illustrated in Figure 1. On the assumption that the relationship should be sigmoidal, the course of percentage survival between 6.5 and 124 ppm. CO₂ (Fig. 1) was interpolated approximately from a

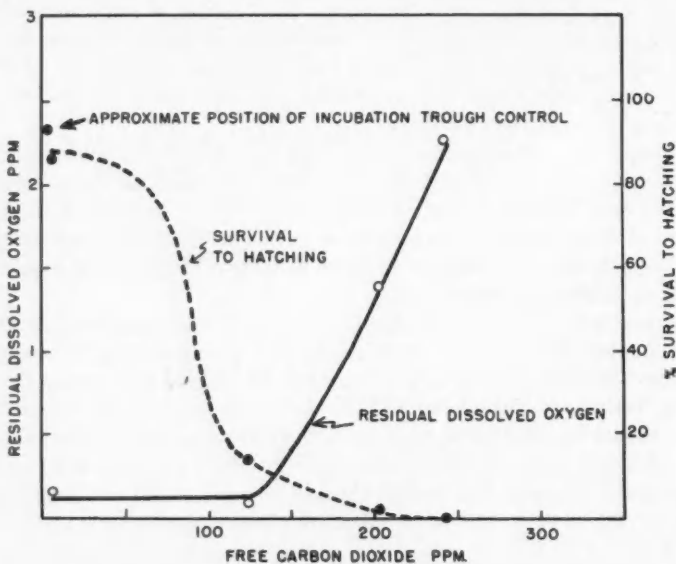


FIGURE 1. Effect of carbon dioxide on the utilization of dissolved oxygen by chum salmon eggs and the recorded percentage live hatch after exposure to 4 carbon dioxide levels in closed bottles for a period of 9 days. Age of eggs at the beginning of the tests was 14 days, or a summed thermal history equivalent to 107.8 Centigrade degree-days. Survival of chum salmon eggs in an incubation trough is noted as a control where free carbon dioxide was less than 5 ppm.

probit plot, since survival should be asymptotic, by analogy with other dose-response relationships, at a level of CO_2 near zero.

DISCUSSION

Salmon eggs of a stage prior to the establishment of pigmented blood and a functional circulatory system are regarded as being dependent entirely on diffusion of respiratory gases across the egg capsule (Krogh, 1942; Hayes, *et al.*, 1951). In order that a gas may diffuse across a membrane, a gradient must exist between the concentrations of the gas on each side of the membrane and the membrane must be permeable to that gas. If the external carbon dioxide pressure is high, the diffusion of carbon dioxide out of the egg may be inhibited. As the period of exposure to carbon dioxide at a low oxygen level was made at a stage prior to the development of blood pigment, it is possible that the main effects on respiration would be concerned with gas transport in the plasma. Since exposure to low dissolved oxygen levels results in a deceleration in development (Alderdice *et al.*, loc. cit.) and a reduction in oxygen consumption (Hayes *et al.*, loc. cit.), a reduction in cellular metabolism undoubtedly occurs.

Black, Fry and Black (1954) subjected 16 species of freshwater fishes to various concentrations of free carbon dioxide and noted the residual oxygen level when fishes respired to asphyxiation in closed containers. The curves relating residual oxygen and free carbon dioxide tensions were suggested as being specific for a given temperature history. For brook trout (*Salvelinus fontinalis*) averaging 17.5 g. in weight oxygen uptake at 17–20°C. was nearly independent of CO_2 level below approximately 170 ppm. CO_2 .

For chum salmon eggs a similar type of relationship exists, oxygen uptake being independent of CO_2 level below about 125 ppm. CO_2 (Fig. 1, solid curve).

Mortality in the experiments is not directly related to the final levels of dissolved oxygen present since mortality was progressively greater at the higher residual oxygen concentrations. Mortality appears to be a function of the inhibition of oxygen uptake by carbon dioxide, resulting in a deceleration of metabolic rate which ultimately is lethal if the inhibiting influence is prolonged. In this respect, pre-circulatory-system salmon eggs may respond to high carbon dioxide levels in the same manner as they respond to low dissolved oxygen levels (Alderdice *et al.*, loc. cit.).

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Polychaeta of the Western Canadian Arctic¹

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ABSTRACT

A summary of the species of Polychaeta hitherto recorded from the western Canadian Arctic is given. Each of the species enumerated is considered in the light of its known, or unknown, occurrence in each of two regions to the west (northern Alaska and the Chukchee Sea) and two to the east (Hudson Bay and Greenland) respectively. The results show an almost complete balance in the number of occurrences of like species in the regions in both directions, suggesting circumpolar distribution within the area studied.

FOURTEEN YEARS AGO we published a short paper dealing with a small collection of Polychaeta made by Sergeant H. A. Larsen, master of the R.C.M.P. Schooner *St. Roch*, during his cruise of 1936-37 in the western Canadian Arctic (E. and C. Berkeley, 1944). We assumed for this purpose a purely arbitrary division of the western from the eastern Canadian Arctic at the 95th meridian of longitude. At that time no other records of Polychaeta had been made in the western region so defined, except by the Canadian Arctic Expedition of 1913-18. Specimens were collected by this expedition between the mouth of the Mackenzie River and Bathurst Inlet, and were reported upon by Chamberlin (1920). Sergeant Larsen's collection comprised 17 species, only 3 of which had been recorded by Chamberlin, but the latter lists several which were not present in Larsen's material. In 1956 we reported (E. and C. Berkeley, 1956) on a collection made by Dr. F. Neave in 1954 off Banks Island and by the personnel of the C.G.M.V. *Cancolim* in the South Beaufort Sea, which added several more species to the previous total. Quite recently we have examined a few specimens collected by Dr. D. V. Ellis at Cambridge Bay which provided the first record of *Haploscoloplos elongatus* from the region together with other species already known there.

In our 1944 paper we made a comparison in tabular form of the species we had recorded from the western Canadian Arctic with their occurrence from regions both east and west of it, at approximately the same latitude, in order to get some idea with which they had the closer affinity. It seems opportune at the present juncture to amplify and extend this comparison. Not only has our knowledge of the polychaete fauna of the western Canadian Arctic increased in the meantime, but so also has that of northern Alaska, thanks to the work of Pettibone (1954) and, going still further west, that of the Chukchee Sea from the work of Ushakov (1952). In the Canadian Arctic east of longitude 95° W. we had in 1944 only the records from the Canadian Arctic Expedition of 1913-18 (Chamberlin, 1920) and our own (E. and C. Berkeley, 1943) from Hudson Bay for comparison. These have now been considerably augmented by the work of the Eastern Arctic Investigations of the Fisheries Research Board of Canada as

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reported by Grainger (1954). It is realized that the records from the Hudson Bay region are derived from more southerly latitudes than those from the other regions now used for comparison, but they are included because they afford the most complete records we have from the eastern Canadian Arctic, and, climatically, the comparisons are justifiable. Wesenberg-Lund's exhaustive reports (1950 and 1953) on the Polychaeta of the west and east coasts of Greenland provide an excellent summary of species which have been recorded from regions approximately as far east of the western Canadian Arctic area as the Chukchee Sea is west of it. We have, therefore, used the records in these reports from between 65° N. and 72° N., on both Greenland coasts, for comparisons in the table which follows, rather than the somewhat scattered records from northern Europe we used in 1944.

All the above mentioned papers are involved in the records given in Table I, the geographical division being as follows:

Western Canadian Arctic	Chamberlin, 1920; E. and C. Berkeley, 1944, 1956.
Northern Alaska	Pettibone, 1954; E. and C. Berkeley, 1956; Chamberlin, 1920.
Chukchee Sea	Ushakov, 1952.
Hudson Bay region	Grainger, 1954; E. and C. Berkeley, 1943; Chamberlin, 1920.
Greenland	Wesenberg-Lund, 1950, 1953.

In addition, the record of *Lagisca multisetosa* from northern Alaska refers to the original description, the locality of which was ascribed by Moore (1902) to Greenland, but subsequently (1905) corrected to Icy Cape, Alaska.

No very exact conclusions can be drawn with regard to distribution from consideration of comparisons such as these because the intensity, as well as the manner, of collecting in the various areas compared may be determining factors. So far as conclusions can be drawn, they contradict our previous conclusion (1944) that the affinities of the western Canadian Arctic species are with those occurring in regions to the east of them rather than to the west. The present data show an almost complete balance between east and west. Out of 54 species recorded from the western Canadian Arctic, 34 have been recorded from the Hudson Bay region and 44 from Greenland (mean = 39) whilst 32 have been found in northern Alaska and 42 in the Chukchee Sea (mean = 37). The distribution seems then to be circumpolar, at any rate between the extremes of longitude of the regions considered.

NOTE ON *HAPLOSCOLOPLOS ELONGATUS* (JOHNSON)

The above record of this species from the Canadian western Arctic is based upon 8 specimens dredged in Cambridge Bay, Victoria Island, by Dr. D. V. Ellis in 5 metres in 1954. The species has not previously been recorded from this region. We recorded it (E. and C. Berkeley, 1956) from Icy Cape, Alaska and suggested that it might well be that some of the specimens classified as *Scoloplos armiger* from the Point Barrow region (Pettibone, 1954) belonged here, since she does not recognize the presence or absence of hooks in the thoracic neuropodia as a differentiating character between *Haploscoloplos* and *Scoloplos*. If this character

TABLE I. List of species of Polychaeta known from the western Canadian Arctic, and their recorded occurrence in four other Arctic regions.

Western Canadian Arctic	Northern Alaska	Chukchee Sea	Hudson Bay region	Greenland
<i>Harmothoe imbricata</i> (Linné)	+	+	+	+
<i>Lagisca multisetosa</i> Moore	+	—	—	—
<i>Evannella impar</i> (Malmgren)	—	+ ^a	—	+ ^a
<i>Antinoe sarsi</i> (Kinberg)	+	+	—	—
<i>Eunoe nodosa</i> (Sars)	+	+	+	+ ^a
<i>Eunoe oerstedii</i> Malmgren	+	+ ^b	—	—
<i>Melaenis loveni</i> Malmgren	+	+	—	+
<i>Gattyana cirrosa</i> (Malmgren)	+	+	+	+
<i>Pholoe minuta</i> (Fabricius)	+	+	+	+
<i>Paranaitis wahlbergi</i> (Malmgren)	—	—	—	+ ^c
<i>Anaitides groenlandica</i> (Oersted)	+ ^d	+ ^d	+	+ ^d
<i>Eleone longa</i> (Fabricius)	+	+	+	+
<i>Eleone flava</i> (Fabricius)	+	+	+	+
<i>Nephtys ciliata</i> (Müller)	+	+	+	+
<i>Nephtys malmgreni</i> (Théel)	—	+	—	+
<i>Castalia aphroditoides</i> (Fabricius)	+	+	—	+
<i>Autolytus prismaticus</i> (Fabricius)	+	+	+	+
<i>Ephesia gracilis</i> Rathke	—	+	+	+
<i>Sphaerodorum minutum</i> (Webster)	—	—	—	+
<i>Onuphis conchylega</i> Sars	—	—	+	+
<i>Lumbrineris similabris</i> Treadwell	—	—	—	—
<i>Lumbrineris fragilis</i> (O. F. Müller)	—	+	+	+
<i>Lumbrineris zonata</i> (Johnson)	—	—	—	—
<i>Haploscoloplos elongatus</i> (Johnson)	+	—	+ ^e	—
<i>Cirratulus cirratus</i> (O. F. Müller)	+	+	+	+
<i>Travisia forbesii</i> (Johnston)	—	+	+	+
<i>Ammochares fusiformis</i> (Delle Chiaje)	—	+ ^f	+ ^f	+ ^f
<i>Myriochele heeri</i> Malmgren	—	+	—	—
<i>Arenicola glacialis</i> Murdoch	+	+	—	—
<i>AxiotHELLa catenata</i> (Malmgren)	—	+	+	—
<i>Praxillella praetermissa</i> (Malmgren)	+	+	—	+
<i>Maldane sarsi</i> Malmgren	+	+	+	+
<i>Eumenia crassa</i> Oersted	—	—	+	+
<i>Spiochaetopterus typicus</i> Sars	—	+	—	+
<i>Flabelligera affinis</i> (Sars)	+	+	+	+
<i>Brada villosa</i> (Rathke)	+	+	+	+
<i>Brada inhabilis</i> (Rathke)	+	+	+	+
<i>Amphicteis gunneri</i> (Sars)	—	—	—	+
<i>Amphicteis sundevalli</i> Malmgren	—	+	+	+
<i>Melinna cristata</i> (Sars)	—	—	+	+
<i>Samytha sexcirrata</i> Sars	+	+	—	—
<i>Asabellides lineata</i> Berkeley ^g	—	—	—	—
<i>Glyphonostomum pallescens</i> (Théel)	—	+	—	+
<i>Cistenides granulata</i> (Linné)	+ ^h	+ ^h	+	+
<i>Capitella capitata</i> (Fabricius)	+	+	+	+
<i>Nicolea zostericola</i> (Oersted)	—	+	+	—
<i>Terebellides stroemi</i> Sars	+	+	+	+
<i>Neomphitrite groenlandica</i> (Malmgren)	+ ⁱ	+	+ ⁱ	+ ⁱ
<i>Leaena abranchiata</i> Malmgren	+	+	+	+
<i>Chone duneri</i> Malmgren	+	+	—	+
<i>Chone infundibuliformis</i> Kröyer	+	+	+	+
<i>Euchone analis</i> (Kröyer)	+	—	+	+
<i>Euchone papillosa</i> (Sars)	—	+	—	+
<i>Dasychone infarcta</i> (Kröyer)	—	+	+	+

^aAs *Harmothoe*. ^bAs *E. barbata*. ^cAs *Anaitis*. ^dAs *Phyllodoce*. ^eAs *H. kerguelensis*. ^fAs *Owenia*. ^gAs *Pseudosabellides*. ^hAs *Pectinaria*. ⁱAs *Amphitrite*.

be disregarded *Haploscoloplos elongatus* and *Scoloplos armiger* come close. However, we cannot agree with the suggestion made by her (1954 and 1957) that these hooks may be worn down capillaries and that their presence or absence depends upon the abrasive quality of the substratum in which specimens are found. In our experience the crotchets, when they occur, have a general shape which excludes any probability of their derivation by abrasion. Hartman (1957) retains the two genera *Scoloplos* and *Haploscoloplos* and gives figures of the hooks of several species of the former. All are of a generally similar type and, in our opinion, quite unlike worn capillaries. We agree with her in regarding the separation of the two genera as a useful one.

The forked setae in *Haploscoloplos elongatus* and *Scoloplos armiger* respectively afford an additional distinction between these two species. In the former the arms of the fork are markedly unequal, tend to diverge, their ends are thickened and grooved, and they are heavily ciliated on the interior edges above the septum (see E. and C. Berkeley, 1952, Fig. 200). In the latter the arms are more nearly equal and parallel, the ends are not thickened and are only obscurely bifid, and no ciliation can be made out.

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The Resistance of Cultured Young Chum and Sockeye Salmon to Temperatures Below 0°C.¹

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ABSTRACT

Recent efforts to establish Pacific salmon in Hudson Bay posed the question of low temperature tolerance in these species. A series of lethal temperature tests at -0.5, -1.0 and -1.5°C. demonstrated that resistance to temperatures slightly below 0°C. was limited. Freezing of the blood and aqueous humour occurred at temperatures of -1.0 and -1.5°C.

INTRODUCTION

IN CONJUNCTION with the planting of chum salmon (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*) into Hudson Bay tributaries², laboratory tests on the tolerance of young salmon to low temperatures in saltwater have been conducted. Since the winter temperatures in Hudson Bay fall as low as -1.6°C. in the upper 50 metres (Hachey, 1954) the possibility of death from freezing was present.

Evidence concerning the ability of fish to withstand temperatures below 0°C. varies according to the species, the conditions of the experiment, and the acclimation state of the fish. Earlier interest was focused on the phenomenon of "anabiosis", or restoration after freezing. Borodin (1932) reported that "fish frozen in a quarter of an hour under a temperature of -14 to -15°C. recovered in most cases, while those frozen during one hour under a temperature of -10 to -12°C. did not revive". (See also Britton, 1924; Borodin, 1934; Schmidt, Plantonov and Person, 1936). A considerable literature exists on cold-tolerance for both cold-blooded vertebrates and invertebrates (reviewed by Luyet and Geheio, 1940). Of more recent interest, the studies of Scholander *et al.* (1953) and Kanwisher (1955) have contributed to an understanding of some of the physiological aspects of cold-tolerance, demonstrating that, for invertebrates, a large proportion of the body fluids can occur in the form of ice without causing permanent injury.

Partially frozen fish survive under some circumstances, but if totally frozen, or locked in an ice blanket, they cannot survive. A remarkable phenomenon of supercooling of the blood in a variety of marine species living naturally at temperatures of -1.73 to -1.75°C. is further reported by Scholander *et al.* (1957). The complete absence of any effective seeding agent has allowed these fish to live quite effectively despite the apparent tenuous circumstances.

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² The Fish and Wildlife Division, Department of Lands and Forests, Ontario, in consultation with the Fisheries Research Board of Canada, undertook the introduction of Pacific salmon in Hudson Bay by planting eyed eggs or fry into several rivers flowing into Hudson Bay and James Bay. The success of this project, commenced in the fall of 1955, will not be known until the life span of the species which matures in 3 to 5 years has followed its full course.

With the exception of a few cases cited above, the majority of systematic experiments performed to determine the resisance of fish to extreme of temperature have been conducted in a medium of fresh water (Brett, 1956). In consequence, determinations have been limited at the lower level by the freezing point of fresh water. Although temperatures *above* 0°C. have proven lethal in many instances, particularly where fish have been acclimated to relatively high temperatures, nevertheless there is a strong suggestion that, where adequate opportunity for acclimation exists, temperatures significantly below 0°C. could be tolerated by freshwater fish. If the temperature tolerance relation for young chum salmon in fresh water were projected by extrapolation (Fig. 4), a temperature of the order of -5°C. would be predicted as the *ultimate lower lethal temperature* (cf. Fry, 1947). Since the freezing point of the blood of salmon is approximately -0.8°C. (Kubo, 1953), this is an unlikely forecast, unless supercooling provides an unexpected degree of protection.

Anadromous fish such as the Pacific salmon present the relatively unique possibility of exploring temperature relations in both fresh and salt water, affording an opportunity of conducting tests below 0°C. In addition both the ecological and fisheries management interest in this problem have stimulated a close examination of the possible consequences to salmon exposed to extremes of water temperature in Hudson Bay.

MATERIALS

THE FISH. Eggs of chum and sockeye salmon collected from two streams in British Columbia were raised by standard hatchery methods in fresh water. Following an early diet of ground beef liver they were fed a composite of 50% canned salmon, 30% liver and 20% "Pabulum", supplemented with yeast and cod liver oil. For chum salmon two stages of development were tested—*fry* at 3 months after hatching, and *fingerlings* 12 months after hatching. The sockeye fingerlings used were approximately 14 months old. Mean fork lengths and weights are recorded in Table I.

TABLE I. Record of size and acclimation history (range shown) for the two species of young salmon used in lethal temperature tests. Chum fry and sockeye fingerlings were held at 7°-8°C., and chum fingerlings at 5.5°-8°C., in stock tanks containing fresh water for about 3 months previous to the start of the acclimation period.

Species	Length	Weight	Temperature history		Salinity history		Lethal test date
			Temp.	Time	Salinity	Time	
	cm.	g.	°C	days	‰	days	
CHUM FRY							
5°C. Acc.	3.4	0.48	4.9±0.3	21	28.8±0.4	21	Apr. 4-5/55
2.5°C. Acc.	3.1	0.33	2.5±0.2	21	28.8±0.4	21	Apr. 4-5/55
CHUM FINGERLINGS							
5°C. Acc.	13.9	23.5	5.0±0.2	49	28.2±1.2	300	Jan. 11-14/56
SOCKEYE FINGERLINGS							
5°C. Acc.	10.5	12.4	4.8±0.3	10	9	10	Mar. 7-10/55
			4.8±0.3	18	28.2±0.4	18	
2.5°C. Acc.	10.7	12.9	2.6±0.2	10	9	10	
			2.6±0.2	18	28.2±0.4	18	

APPARATUS. The lethal temperature tanks, used for testing *minimum* temperature tolerance in this instance, were very similar to those described by Brett (1952). Temperatures were controlled to within 0.1°C . by thermo-regulating a glass-encased 80-watt heater balanced against an enclosed frozen-brine cooler (Fig. 1). Because of the reduced activity of the fish and the need for close inspection for determining the time of death, a shallow, fine-meshed, nylon net bag was suspended in the centre of the tank. Fish placed in the bag were subject to slow circulation of water produced by a stirrer and tubular aerator.

A gradual daily exchange of water, equal to approximately twice the volume of the tank (23 liters) was introduced into each of the five insulated tanks.

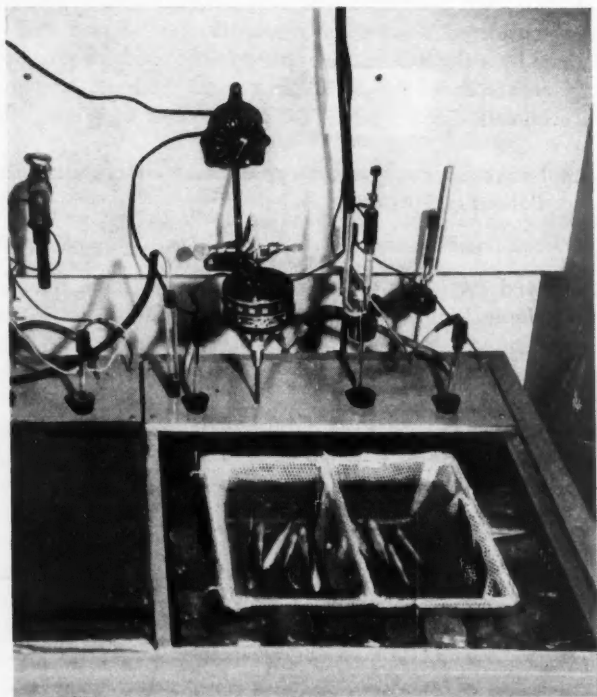


FIG. 1. A view of the lethal temperature tanks with insulated lid removed from one bath. Dead sockeye at a temperature of -0.5°C . are shown. Temperatures were reduced by the use of frozen brine.

METHODS

ACCLIMATION. The salinity and temperature histories of the fish are recorded in Table I.

The stock of chum fry originated from a small stream draining directly into the ocean (Nile Creek, Vancouver Island). They normally migrate to sea as fry, and are subject to a relatively high salinity at an early stage. Young sockeye do

not usually leave fresh water until the spring of their second year. The salinity histories of the experimental fish were patterned accordingly.

Two levels of temperature acclimation were chosen, 5°C. and 2.5°C. Since tolerance tests were conducted in midwinter and early spring, the temperatures of the stock tanks were comparatively low, so that the new imposed acclimation levels involved a reduction of no more than 4 to 5 degrees at most.

LETHAL TEMPERATURE EXAMINATION. The methods employed were essentially similar to those described in an earlier paper (Brett, 1952). Test temperatures of -0.5°, -1.0° and -1.5°C. were employed, transferring 10 fish in small glass containers directly from the acclimation troughs to the lethal tanks. Salinities were maintained at 28‰.

Fish were considered dead when respiration had ceased and no response could be obtained by a slight pressure applied to the caudal peduncle. This stage was frequently accompanied by a stiffening of the body. Each sample was returned to its acclimation temperature for a period of 24 hours. No recoveries occurred.

Water samples taken for oxygen content, determined by the standard Winkler method, averaged about 11.5 p.p.m.

RESULTS

No fish survived even the -0.5°C. temperature for more than 3 days. The median tolerance limits are recorded in Table II and Fig. 2.

TABLE II. Median resistance times to low temperatures in two species of young Pacific salmon. Times determined graphically by interpolation, as in Figure 3.

Species	Stage	Acclimation temperature °C.	Median resistance times at lethal test temperatures		
			-1.5°C. <i>min.</i>	-1.0°C. <i>min.</i>	-0.5°C. <i>min.</i>
Chum	fry	2.5	26	430	1320
		5.0	40	335	1050
	yearling	5.0	11	26	2800
Sockeye	yearling	2.5	26	28	2350
		5.0	26	28	2900

Chum fry died very rapidly at -1.5°C. and -1.0°C. (Fig. 3A and B). A marked change in the slopes of the lines relating the order of death (probit) to the time of death (logarithm) indicated the possible existence of two mechanisms involved in low temperature resistance.

A somewhat similar relation occurred in the chum yearling mortalities (Fig. 3C). At -1.0°C. "delayed mortality" occurred, similar in all respects to that obtained when studying low lethals in young salmon cultured in fresh water, and tested at temperatures between 0° and 3°C. (15° to 23°C. acclimations—Brett, 1952). This type of response, originally described by Doudoroff (1942) as "primary and secondary chill-coma" appears to be relatively common in the

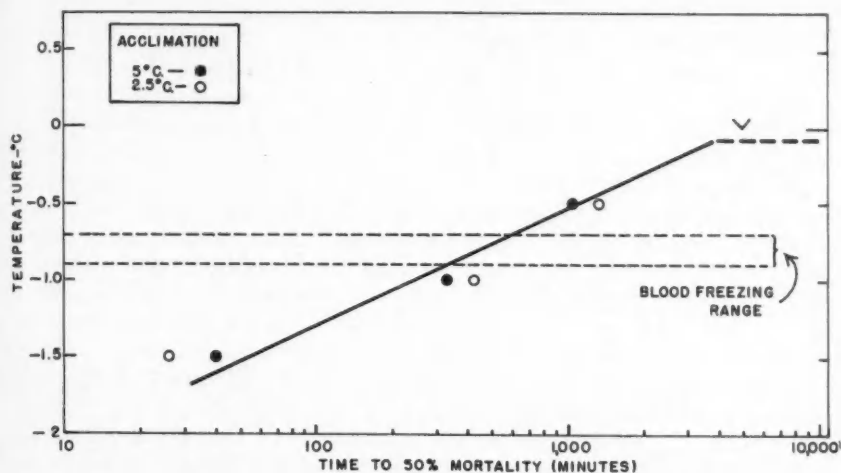


FIG. 2. Medium resistance times to temperatures below 0°C. for chum salmon fry. "V" indicates a resistance greater than 5,000 minutes at a temperature of 0°C., determined in earlier experiments (Brett, 1952). In general, results for experiments performed for 4,000 minutes or more show little change by comparison with longer exposure times. Hence, in the above figure, the extrapolation has been made to an exposure time of 4,000 minutes.

phenomenon of resistance to cold. The hypothesis is that rapid penetration of cold, affecting the central nervous system, accounts for the primary phase. These rapid deaths were characterized by contortions and violent responses. The secondary coma is thought to be associated with systemic disorder, possibly arising from inadequate osmotic control. At -0.5°C. the leached appearance of many of the fish which lasted for some hours in the hypertonic salt water tanks (28‰) would support the latter supposition. At lower temperatures death was obviously associated with rapid freezing. Ice crystals formed in the aqueous humour of the eye in a matter of minutes at -1.5°C. The lens became clouded, causing cataracts. At -1.0°C. a similar condition was apparent in the eyes of some of the fish, and a rapid stiffening of the body occurred, though not in every instance. Since the freezing point of the blood of adult salmon in salt water is about -0.75 to -0.90°C. and that of the smolt from -0.70 to -0.76°C. (Kubo, 1953), freezing would occur unless super-cooling could be maintained. Inspection of the sinus venosus revealed large ice crystals entirely blocking the chamber. Although these could have been seeded by the act of handling the fish, the stiffened body and readily observed freezing of the aqueous humour in untouched fish indicated that ice formation occurred readily at temperatures slightly below the blood freezing point. By comparison the kidney did not appear to be frozen, which could be related to the presence of a hypertonic urine.

The resistance of the sockeye yearlings to a temperature of -0.5°C. was approximately the same as that for the chum yearlings (Fig. 3C). Lower temperatures, however, showed more severe effects on the sockeye.

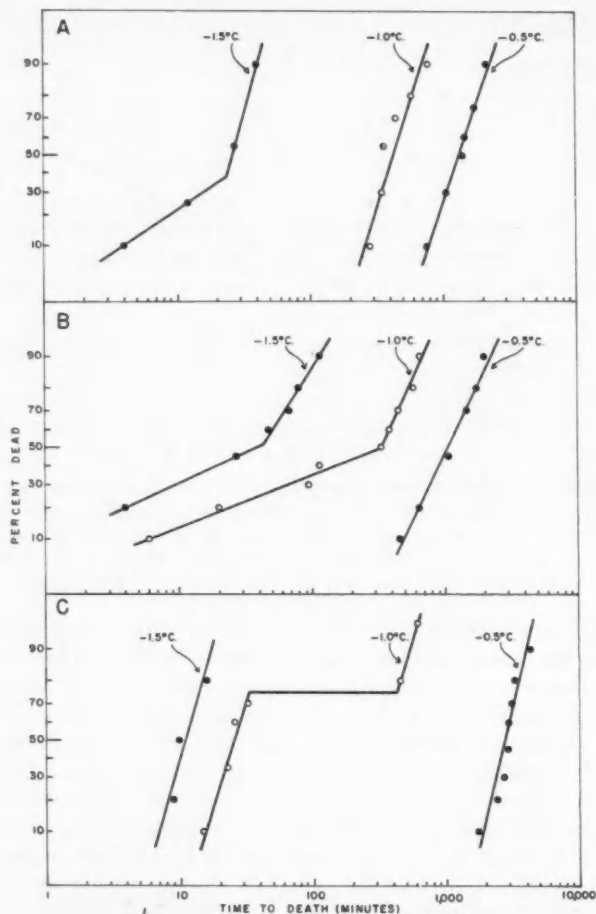


FIG. 3. Times of death at various low temperatures for chum fry acclimated to 2.5°C. (A) and 5°C. (B), and for chum yearlings acclimated to 5°C. (C). Plotted on probit \times logarithmic axes.

In almost every case the 5°-acclimated samples showed equal or greater resistance to cold than the 2.5°-acclimated samples. From this it can be inferred that the 2.5°C. acclimation temperature imposed a slight stress which was reflected in greater susceptibility when a severe cold stress was imposed.

DISCUSSION

The systematic examination of the relation of lethal temperature to acclimation temperature, given such impetus by the work of Fry and associates (Fry *et al.*, 1942; Fry, 1947) led to establishing a zone of tolerance, equal to the area enclosed

by the lines relating the upper and lower lethal temperatures to acclimation temperature (Fig. 4). The *theoretical* upper ultimate lethal temperature never occurred in fact since a plateau was reached beyond which further elevation of the acclimation temperature provided no increase in tolerance. In the freshwater species studied, the lower limits were truncated by the freezing point of water. An extrapolation of the relation, as stated earlier, suggested a theoretical lower limit of the order of -5°C . for a salmonid such as the chum salmon. Since this was below blood freezing point it appeared a highly unlikely proposition. In the present instance the actual ultimate lower limit is very close to 0°C . for both species, so that the zones of tolerance determined previously (Brett, 1952) are virtually equal to the ultimate zones of tolerance.

In view of the existence of marine fish at -1.7°C ., reported by Scholander *et al.* (1957), it would be of interest to determine the ultimate lower lethal levels in arctic species, including the Arctic char (*Salvelinus alpinus*). This latter species appears to avoid the more severe winter temperature of the sea by entering freshwater streams and lakes protected from freezing by the insulating sheet of ice and snow (Andrews and Lear, 1956).

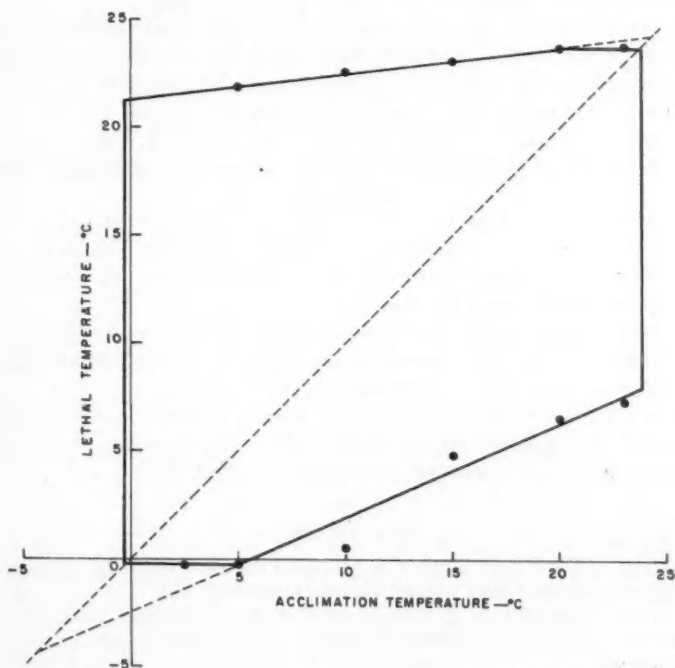


FIG. 4. Tolerance diagram for young chum salmon. Lower lethal temperatures for 2.5 to 5.0°C. acclimations determined in this paper, the balance from earlier experiments (Brett, 1952).

Chum salmon ascend arctic rivers as far west as the Lena River of Siberia, and as far east as the Mackenzie River of Canada, although not in large numbers (Dymond and Vladykov, 1934; Berg *et al.*, 1949). These must pass through waters which in winter would have freezing temperatures comparable with those of Hudson Bay. Without direct proof it must be surmised that the young fish migrate out of these Arctic waters during their first summer of marine life, and that the adults likewise avoid the severe winter temperatures on their return migration.

The possibility of survival of the stocks of chum and pink salmon planted in rivers draining into southern Hudson Bay hinges on the occurrence of one or the other of several rather unlikely events. Either the salmon could migrate (without previous local conditioning of their stocks) hundreds of miles northeast through the Bay and south in the Labrador current, or they might resist the cold by maintaining a super-cooled state, or they might return to the shelter of fresh or brackish water each winter while immature. While none of these eventualities seemed likely, none was completely impossible *a priori*, and *one* only was needed for success in this phase of the operation. The plantings were made because of the great potential importance of a successful result, and in full awareness that failure was more likely than success.

The factual story is not yet complete, since the chum salmon would only reach their 4th year in the autumn of 1958, and a 5th year would still hold possibilities of returns to the Hudson Bay "home streams". No trace of the pink salmon, which should have returned as 2-year-old mature fish last fall, has been reported (H. H. Mackay, personal communication). The fate of those plantings has probably already been sealed by the arduous environment of Hudson Bay.

SUMMARY

Low lethal temperature tests on young chum and sockeye salmon revealed a complete intolerance to temperatures of -0.5°C . and lower. The mean resistance times indicate that a temperature of -0.1°C . approximates the ultimate lower lethal temperature for young salmon.

At temperatures below the freezing point of the blood, freezing of the aqueous humour occurred in untouched fish. There was no indication of resistance through maintaining a super-cooled state.

The possibility of survival of planted stocks of chum and pink salmon in Hudson Bay would hinge on migration out of the Bay before the sub-zero temperatures of ice-covered winter conditions prevailed.

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Some Observations on the Structure and Photomechanical Responses of the Pacific Salmon Retina¹

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ABSTRACT

The general structure of the Pacific salmon retina is described. Rods, single cones and twin cones constitute the visual cell layer which, together with the dense pigment layer, undergoes photomechanical changes common to most teleosts. Stages in the contraction and expansion of rods and cones, and the migration of pigments are depicted.

In the laboratory, cultured sockeye salmon became well light-adapted in 20–25 minutes, whereas the time for dark-adaptation was of the order of 55–60 minutes.

In the Lakelse River, a sample of natural-run sockeye and coho smolts was found to be fully dark-adapted by about 10:00 P.M. when the light intensity at the water surface was 0.03 foot-candle. Pink and chum fry from Hooknose Creek were similarly dark-adapted by about 9:45 P.M. on an evening when the intensity had fallen below 0.002 ft.-c. At the start of evening migration retinal dark-adaptation in sockeye smolts had just started, whereas in pink and chum fry the retina was approximately half dark-adapted when migration commenced.

INTRODUCTION

THE STRUCTURE AND HISTOLOGY of the teleost eye have been described for a wide variety of species (Wunder, 1936; Walls, 1942; Detwiler, 1943; Rochon-Duvigneaud, 1943; von Studnitz, 1952; von Buddenbrock, 1952), and recently a general review of the physiology has been compiled by Brett (1957). With the exception of experiments conducted by Wald (1941) on the visual pigments of *Oncorhynchus*, there is no detailed description of the visual mechanism in this genus. Many of the salmon's activities have been shown to depend on its visual responses (Neave, 1955; Fields *et al.*, 1955; Hoar, 1956; Brett and Alderdice, 1958) and comparative studies may be expected to contribute to an understanding of the mechanisms involved. In this investigation a histological study of the retinae of the five species of *Oncorhynchus* (sockeye, *O. nerka*; coho, *O. kisutch*; chum, *O. keta*; pink, *O. gorbuscha*; and chinook, *O. tshawytscha*) was undertaken. The histology of the retina in its light- and dark-adapted conditions was considered first. This formed the cellular basis for examining rates of visual adaptation in the laboratory and provided a comparative index for stages of adaptation during natural migration.

MATERIALS AND METHODS

SOURCE AND SIZE OF FISH. Pacific salmon fry and fingerlings used in studies of the structure of the retina and the rates of light- and dark-adaptation under laboratory conditions were cultured from fertilized eggs. All the laboratory samples were taken from aerated, running, fresh water, with temperatures usually

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varying between 12°C. and 15°C., but sometimes reaching extremes of 20°C. in summer to 8°C. in winter. Field samples were obtained at counting weirs maintained in the outlet streams of two coastal British Columbia lakes, Lakelse (Skeena River drainage) and Port John (on King Island). Table I summarizes age, length and weight data.

TABLE I. Age (from hatching) and approximate length and weight of young Pacific salmon used for eye sectioning.

Species	Stock	Age	Length	Weight
		<i>months</i>	<i>cm.</i>	<i>g.</i>
Pink fry	Cultured	4+	3.5-3.9	0.4-0.5
Chum fry	"	4+	3.5-3.9	0.4-0.5
Sockeye fry	"	4+	3.5-3.9	0.4-0.5
Coho yearlings	"	15-18	10-12	18-22
Chinook yearlings	"	15-18	10-12	18-22
Sockeye yearlings	"	15-18	10-12	18-22
Pink fry	Wild	4	3.4	0.4
Chum fry	"	4	3.9	0.5
Coho yearlings	"	15	11.4	21
Sockeye yearlings	"	15	10.2	18

HISTOLOGICAL METHODS. For examination of the general retinal structure, fish were anaesthetised with chlorotone prior to removal of both eyes. The excised eyes were then placed in Bouin's fixative for one day. After hardening, a small slit could be made in the cornea, and the lens removed. Each eye was next washed in 70% alcohol with a small amount of lithium carbonate added to remove the picric acid. The material was then dehydrated, cleared in xylene, and embedded in paraffin.

Sections were usually cut at 6 μ and 8 μ , subsequent to staining with Harris' haematoxylin and eosin. A few preparations were de-pigmented to facilitate study of the rods and cones specifically. The rods in particular require such techniques since they are masked by the epithelial pigment in light-adapted eyes. Mayer's (1881) and Arey's (1916) methods were used, observing the fact that de-pigmented material must be stained much longer because of acid treatment.

LIGHT-ADAPTATION. Two experiments on the rate of light-adaptation in young sockeye were conducted. Samples of the fish were left in total darkness for 4 days before exposure to bright light (6,300 ft.-c.) during the night. This step was taken to avoid the possible influence of diurnal rhythm of mechanical movements in the retina which have been observed by Welsh and Osborne (1937) to persist up to 4 days in the absence of any stimulus from a light source.

The primary experiment, with yearlings, was conducted in July, 1955. After fixing the first sample in total darkness, the remainder were fixed after 2, 4, 8, 16, 32, 64 and 128 minutes direct exposure to light. The second series, with fry, was conducted a year later, using the following intervals of exposure: 1, 2, 3, 4, 6, 8, 24, 32, 40, 52, 64, 76 and 90 minutes. Sampling intervals were changed in the second experiment because the results of the first series indicated that the process of light- and dark-adaptation was very nearly complete in about 30-50 minutes.

DARK-ADAPTATION. Experiments on the rate of dark-adaptation were performed with both sockeye fingerlings and fry, during the day. Fish were sampled at the same intervals as in the light-adaptation experiments, subsequent to exposure to continuous bright light (6,300 ft.-c.) for 4 days. After fixing the first fish under this light intensity, the remainder were maintained in absolute darkness, and sampled at the prescribed intervals.

SAMPLING OF MIGRATING YOUNG SALMON. The sockeye and coho smolts sampled at Lakelse Lake were taken directly from the counting weir during migration, and immediately fixed in Bouin's. The water depth in the traps was about 120 cm. Surface light intensity readings at the time of sampling were made with a Photovolt photometer (No. 210 M), filtered for the "standard observer". Samples were fixed at the following times—6:00, 7:00, 8:00, 8:30, 9:00, 9:30, 10:00 and 10:45 P.M., Pacific Standard Time.

Migrating pink and chum fry, just emerging from the gravel, were taken as they entered the Port John weir, appropriate samples being bottled at regular intervals of 15 minutes until 11:30 P.M. Some pink fry were used as "controls". These had been captured the previous evening and maintained under natural light in an aquarium. They were sampled every 15 minutes from 8:00 to 11:30 P.M. with accompanying measurements of light intensity.

MEASUREMENTS. Measurements of the thickness of the retina (choroid to external limiting membrane), the external nuclear layer, and the internal nuclear layer (Fig. 4), were made in the regions of the ora serrata,³ the fundus, and between the ora serrata and fundus, using an ocular micrometer. Since the rods and cones undergo photomechanical changes only in that portion of the cell proximal to the external limiting membrane, they were consequently measured from that membrane to the tips of their myoids (Fig. 1).

The thickness of both pigment and cone layers was also recorded. The region from the edge of the choroid to the tip of the pigment protuberances was used as a measure of the pigment layer. Measuring the rods was not only difficult but also appeared to be somewhat unreliable due to their smallness and the masking effects of the pigment epithelial cells in the light-adapted retinae. It was felt that the measurement of the thickness of pigment and cone layers was adequate to provide a good measure of rates of light- and dark-adaptation. Since the thickness of the various layers varied with the size of the retina, each measurement was expressed as a percentage of the retinal thickness. This latter figure has been used in all comparisons (see Figures 5 to 8).

GENERAL STRUCTURE OF THE RETINA

THICKNESS OF THE RETINA

The individual retina in teleosts is known to vary in thickness from less than 100 μ to more than 500 μ (Walls, 1942). It is thickest in the region of the fundus and thinnest at the ora serrata, mainly as a result of decreasing thickness in the

³The posterior portion of the eye where the retina is thickest is referred to as the fundus, and the periphery as the ora serrata.

nerve fibre layer. In the case of salmon fry, the thinnest retinae measured about $196\ \mu$ and the thickest $336\ \mu$. Among the yearlings, the range was from $200\ \mu$ to $450\ \mu$. The average thickness in the region of the fundus was approximately $300\ \mu$. It is of interest to compare this with the retinal thickness (near fundus) in the guinea pig ($130\ \mu$), bat ($133\ \mu$), hamster ($182\ \mu$), catfish ($182\ \mu$), chameleon ($442\ \mu$), hawk ($400\ \mu$), owl ($389\ \mu$), and man ($390\ \mu$) (Detwiler, 1943). Detwiler states that the same fixative (modified Held's) was used to preserve each of the above-mentioned eyes in order to avoid differential shrinkage due to the use of different fixatives. The delicate retina is easily disturbed by fixatives and some shrinkage invariably occurs. However, by using the same fixative, uniform shrinkage can be obtained, hence the same histological methods were used throughout the present study.

PIGMENTED EPITHELIAL LAYER

The pigment epithelium consists of a regular layer of cells in a single row (Fig. 1). The cells possess long, finger-like processes extending well into the visual cell layer. The outer portion of the cell is adjacent to the choroid, close to which its rather spherical nucleus lies. The pigment in the upper part of the cell, around the nucleus, is granular and apparently not subject to intra-cellular movement. The pigment in the processes, on the other hand, is needle-shaped and migrates within the cell processes. In the dark-adapted retina, the needle-shaped pigment granules lie close to the granular pigment, leaving the processes vacant and transparent.

Teleosts as a group have thick, heavily-pigmented epithelial layers, and *Oncorhynchus* is no exception. This dense layer extends almost to the external limiting membrane in the light-adapted retina, masking the rods and even extending around the retracted cones. In the absence of a contractile iris the full expansion of the pigment in the light-adapted condition would appear to provide a very efficient control of the amount of light coming in contact with the visual elements. The pigmented epithelial layer is virtually uniform in its thickness, except at the very tip of the ora serrata, where it tapers off abruptly.

VISUAL CELL LAYER

As in the case of most teleosts studied, the visual cell layer of *Oncorhynchus* consists of three types of receptors, namely twin cones, single cones, and rods (Fig. 1).

CONES. The twin cones of *Oncorhynchus* consist of two nuclei inside the external nuclear layer, lying close to the external limiting membrane. The myoid passes through the external limiting membrane and extends to the base of the ellipsoids and is the part of the cell that expands and contracts during photo-mechanical responses. Arey (1915, 1916) observed that the maximum ratio of fully expanded to contracted myoid in fishes may be 10:1. A ratio of this order was apparent in *Oncorhynchus*. The single cones are like the individual elements comprising the twin cones, except that their myoid and ellipsoids are separate.

The cone ellipsoids are barrel-shaped, which, together with the outer segments, provide the pear-shaped outline of the cone. The ellipsoids of the twin cones which are attached to one another have separate outer sections.

The cones varied considerably in size and, in the light-adapted condition, ranged from 21.6μ to 35.2μ in length (from external limiting membrane to tip of outer segment). In the dark-adapted condition, they varied from 39.2μ to 76.2μ . The average breadth of the cone ellipsoid was 5.5μ and the outer segments 2.6μ . In sections which were 8μ in thickness, 9 twin cones and 10 single cones were found in an area of $100 \mu^2$. The cones are arranged in neat square-shaped mosaics, the twin cones forming the sides and the single cones forming the corners with another single cone in the centre. Although this was the general pattern, in the peripheral region cones were sometimes seen to be arranged in rows.

Rods. The rods are built on the same general plan as the cones except they are long and slender, measuring about 2μ in breadth. They varied in length from 20 to 25μ in the dark-adapted condition to between 80 and 90μ in the light-adapted state. The number of rods in the different regions of the retina varied. In the region of the fundus, they were fewer (12 ± 2 for $100 \mu^2$) than near the ora serrata (15 ± 2).

ACCOMPANYING LAYERS AND MEMBRANES (FIG. 4)

EXTERNAL LIMITING MEMBRANE. This very thin, but usually clearly visible membrane, lies between the visual cells and the external nuclear layer. In some sections it is not distinctly seen in the peripheral regions.

EXTERNAL NUCLEAR LAYER: Lying between the external limiting membrane and the external molecular layer, this layer contains the nuclei of the visual cells. The more circular nuclei, lying immediately adjoining the external limiting membrane, belong to the cones, while the smaller almost oval ones are the rod nuclei. The thickness of the external nuclear layer ranges from 20.8μ to 27.2μ . Walls (1942) observed that this layer is much thicker than the internal nuclear layer in nocturnal animals, whereas the opposite relation occurred in diurnal species. In *Oncorhynchus* the external nuclear layer is thinner than the internal nuclear layer (sometimes half as thick), even though it is not completely a diurnal fish. Such a relation may be due to the presence of a large number of cones in its retina.

EXTERNAL MOLECULAR LAYER. This is a very transparent and lightly staining, reticular layer with a few darkly staining tips of rod and cone bipolar cells, together with foot pieces of cones and smaller ones of rods.

INTERNAL NUCLEAR LAYER. As mentioned earlier, in *Oncorhynchus* the internal nuclear layer is almost twice as thick as the external nuclear layer, measuring from 34 to 40μ . The internal nuclear layer consists of the bipolar cells, stellar ganglion cells and amacrine cells. Details of their structure are not revealed with routine histological methods. Franz (1913) has given a detailed description of the neurological arrangement in the teleost retina.

INTERNAL MOLECULAR LAYER. This broad and transparent reticular layer is almost twice as thick as the internal molecular layer and stains very lightly.

GANGLION CELL LAYER. This layer in *Oncorhynchus* is about one cell deep and consists of a chain of granular, spherical cells, with a surrounding reticular structure.

NERVE FIBRE LAYER. Composed of the fibres leading to the optic tract, this is a highly transparent layer which is thickest near the fundus and gradually decreases in thickness towards the ora serrata. At the periphery it is reduced to a very thin layer.

INTERNAL LIMITING MEMBRANE. This thin layer forms the inner border of the retina in the optic cup.

SIMILARITY OF RETINAE

An extensive microscopical examination of the retinae of all species did not reveal any structural differences or distinctive pigment distribution which could serve to distinguish the species. If such a distinction exists, it is apparent that a rigorous study involving numerous measurements and appropriate analysis would be required before detailed differences could be determined.

PHOTOMECHANICAL RESPONSES

In the light-adapted eye of *Oncorhynchus* (Fig. 1, 2D, 3A, 4), the pigment has migrated fully into the processes of the pigment epithelial cells and almost enveloped the outer segments of the cones, which are completely contracted and lie adjacent to the external limiting membrane. The rods, on the other hand, are expanded and cannot be seen unless the pigment is bleached.

In the dark-adapted state (Fig. 2A, 3D) the pigment is fully contracted. The contraction is so complete in some histological sections that it forms a line of cleavage so that the pigment peels away from the rest of the retina when sectioned. The rod myoids have shortened and the cones have elongated through the relaxation of their myoids. In this state the cones are seen to lie close to the contracted pigment which is in the form of a dense, compact strip lying immediately adjacent to the choroid.

No changes either in the form or staining reactions of external and internal nuclear layers in response to light or darkness were observed. Garten (1907) found that in *Abramis* and *Leuciscus* light decreased the staining of the nuclei in the external nuclear layer, but Chiarni (1904) considered this doubtful, and in *Leuciscus* no decrease of chromatin was found in the internal nuclear layer when subjected to light and practically no changes were noted in the ganglion cells.

LIGHT-ADAPTATION

An almost immediate response of both pigment and cones was observed when the totally dark-adapted fish were exposed to bright light (Fig. 5). The change in these layers continued rapidly for 16-18 minutes, reaching an advanced stage of light-adaptation by 20-25 minutes. There was less variation in response among

the older fish (fingerlings), which may be partly attributed to the relative accuracy of measurements possible in a larger eye.

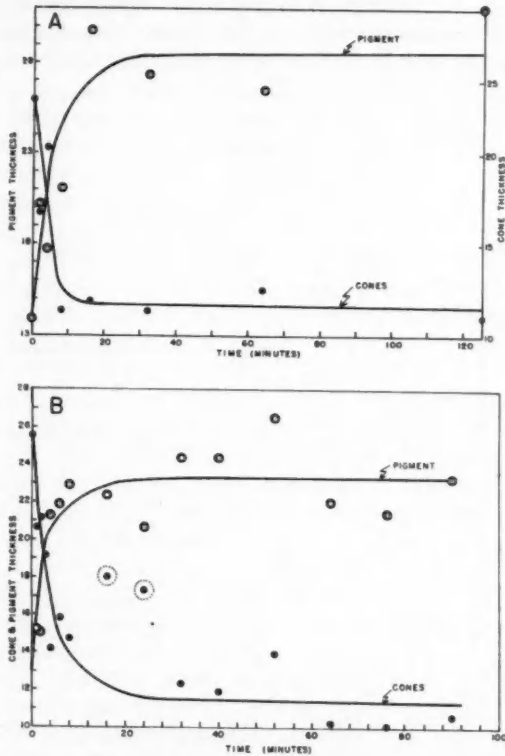


FIGURE 5. Light-adaptation in sockeye fingerlings (A) and fry (B). The progress of change in the thickness of the cone and pigment layers when exposed to strong incident light after 4 days in total darkness is shown. The pigment is migrating into the processes of the protective epithelial cells, while the myoids of the cones are contracting. Compare with Fig. 2. The thickness of each layer is expressed as a percentage of the total thickness of the retina in each case. The encircled points for cones (B) are considered aberrant in view of results obtained in A.

A general examination of the sections revealed that the rods reacted to light at a somewhat slower rate. They appeared nearly half expanded after about 15 minutes and attained maximal expansion in about 40 minutes.

By comparison the pigment in *Ameiurus*, *Abramis* and *Fundulus* attained maximal expansion in 45 minutes to one hour, while the cones (*Abramis*) and rods (*Ameiurus*) were light-adapted in approximately 45 minutes (Arey, 1916).

DARK-ADAPTATION

In the dark, the pigment layer did not "contract" with the degree of rapidity which it showed in "expanding" when exposed to light (Fig. 6). After a latent period of about 20 minutes pigment migration was observed. The half-way stage was reached in approximately 30 minutes, with maximal retraction by 60 minutes.

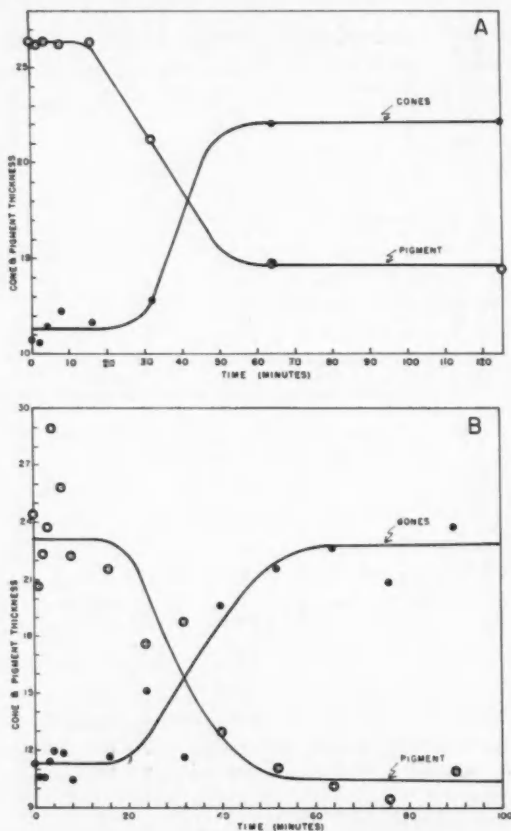


FIGURE 6. Dark-adaptation in sockeye fingerlings (A) and fry (B), when placed in total darkness following exposure to bright light. Here the reverse of the process in light-adaptation occurs. Pigment migrates back into the body of the epithelial cells, and the myoids of the cones extend, increasing the thickness of this layer. Note the initial latent period, as indicated in Fig. 3. Thickness expressed as in Fig. 5.

In general, 24 minutes after exposure to dark, the pigment became less dense and spaces occurred between cell processes (Fig. 3B). When the pigment was approximately $\frac{1}{2}$ -“contracted”, the spaces diminished, while the pigment became

denser finally migrating out of the processes forming a dense, thin strip (Fig. 3D). Arey (1916) states that in *Ameiurus* and *Fundulus*, pigment migration was complete in about an hour after exposure to dark, but in *Abramis* the same stage was reached in roughly half that time.

The cones, like the pigment, did not respond immediately on exposure to dark. No expansion was noted for almost 20 minutes. After this, expansion was appreciable. The half-expanded stage was reached in about 35 minutes and maximal expansion in from 55 to 60 minutes. This is distinctly longer than it takes for the cones of *Abramis* (30 minutes) to elongate in the dark (Arey, 1916).

In an examination of the sections it was observed that the rods, unlike the cones and pigment, showed an immediate response on exposure to darkness. They were half-contracted in about 15 minutes and attained the fully dark-adapted condition after about 25 minutes. Arey (1916) recorded that in *Ameiurus* maximal contraction of the rods in darkness occurred in 30 minutes.

ADAPTATION STATES DURING MIGRATION

Because of the latent periods of response in the photomechanical movements in cone and pigment dark-adaptation, obtained under laboratory conditions, it is difficult to determine from the field records just when the process commenced (Fig. 7, 8). However the examination of movement in the rods suggests some contraction between 8 and 9 P.M. corresponding with the other cell movements (Table II). Since light fades at evening time, at varying and irregular rates depending on cloud coverage, there is a marked difference between the sudden cessation of bright light in the laboratory studies and the relatively gradual diminution in nature. The duration of the latent period, therefore, cannot be directly applied to the field records.

The time at half adaptation is the most reliable figure, being more readily determined. In all cases this occurred between 9:00 and 9:45 P.M. when the light intensity had dropped to at least 15 ft.-c. (sockeye) or below the level of sensitivity of the meter (.002 ft.-c.) as in the case of chum fry. Light intensity figures have only relative significance since different water depths are concerned and the migrants have various behaviour patterns in relation to their cover responses. In most instances dark-adaptation was apparently complete between 9:30 and 10:00 P.M.

OBSERVATIONS AND DISCUSSIONS

GENERAL HISTOLOGY. The retina of *Oncorhynchus* is typical of teleosts capable of bright- and dim-light vision. The thick, dense pigment layer and large number of cones, resulting in the external nuclear layer being thinner than the inner nuclear layer, signifies a capacity for diurnal vision. The abundance of rods and extensive pigment migration also indicate an adaptable eye for varying light conditions.

Twin cones are known to occur only among the teleosts (Walls, 1942). Entire retinæ or regions of retinæ in some forms possess one or two types of these cells. Generally, deep-sea forms have pure rod retinæ, while surface forms have single and twin cones and rods. Wunder (1925) suggested that the presence

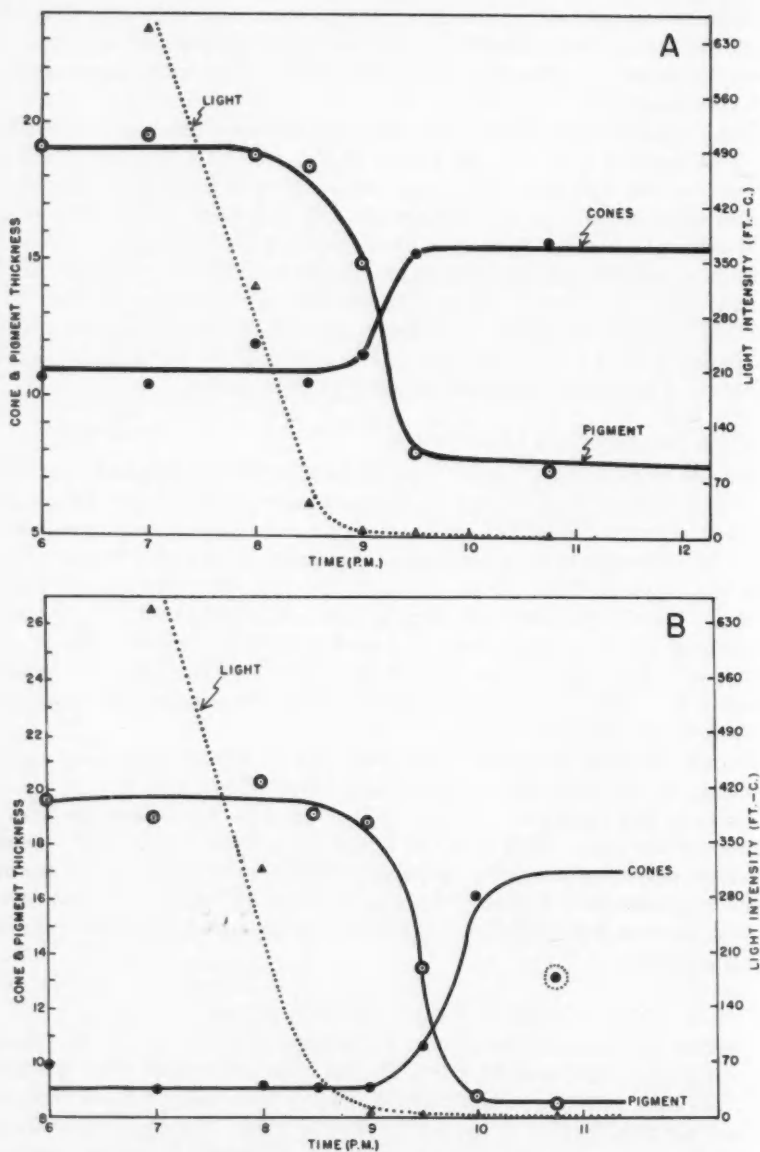


FIGURE 7. The pattern of dark-adaptation as it occurred in migrating sockeye (A) and coho (B) fingerlings with the onset of darkness, in the Lakelse River. The change in light intensity at the water surface during the time of migration is shown. The peak pulse of evening migration coincides with the time of most rapid photo-mechanical responses, between 9 and 10 P.M. Thickness expressed as in Fig. 5. The circled point for cones in B is considered aberrant.

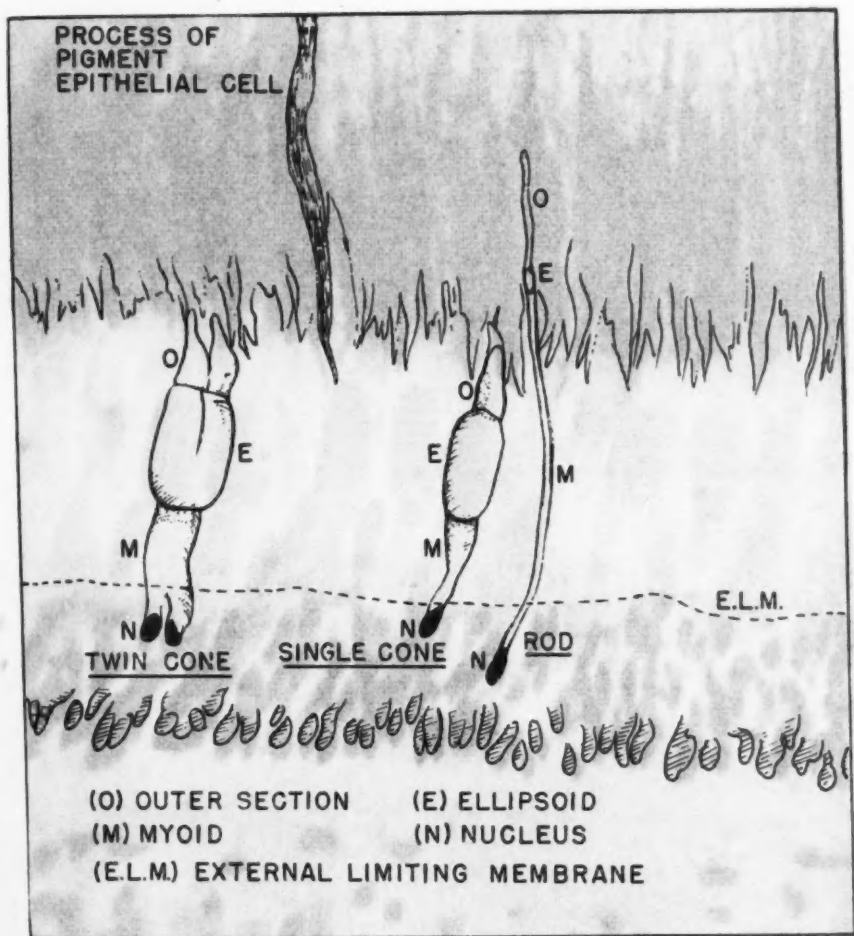


FIGURE 1. Light-adapted retina of a young toad, showing the pigment migrated into the finger-like processes of the pigmented epithelial layer, shielding the extended rods. The cones are in the advanced position with myoids fully contracted ($\times 500$, 3 min. Harris' haematoxylin and 5 min. alcohol eosin).

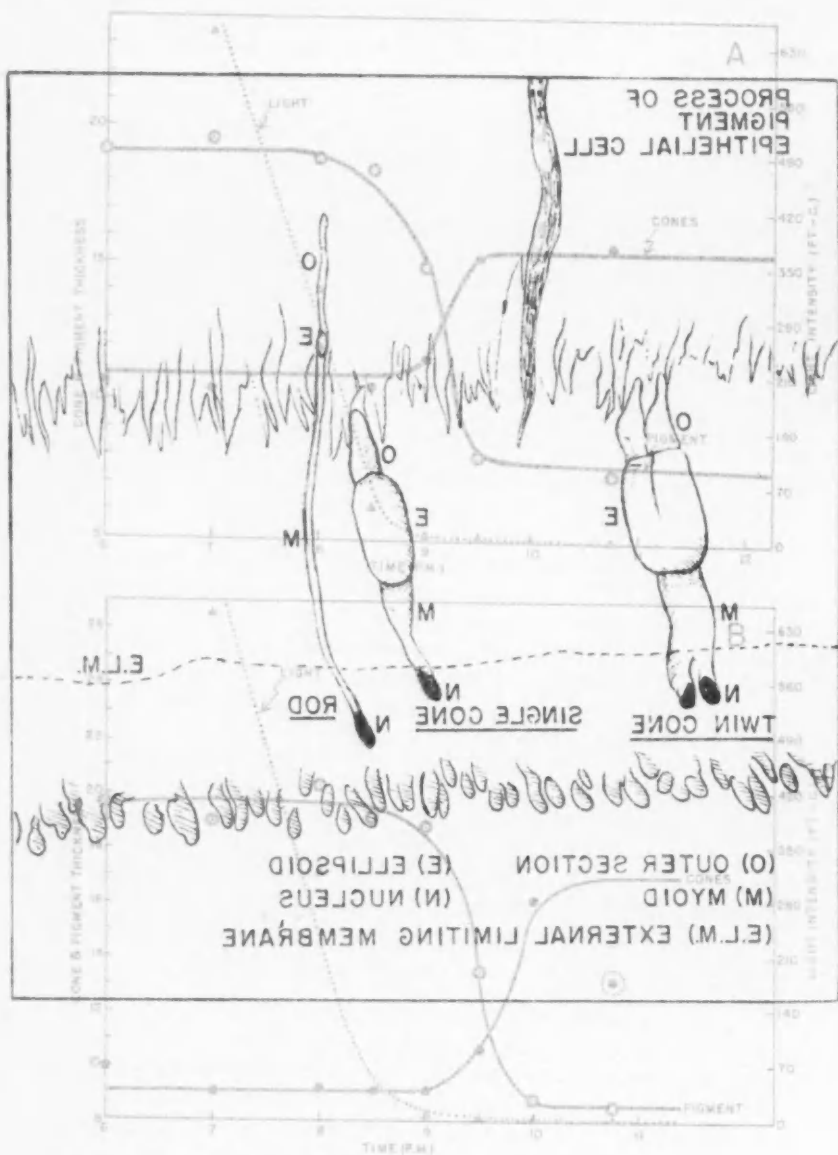


FIGURE 7. The pattern of dark-adaptation as it occurred in migrating sockeye (A) and coho (B) fingerlings with the onset of darkness, in the Lakelse River. The change in light intensity at the water surface during the time of migration is shown. The peak pulse of evening migration coincides with the time of most rapid photo-mechanical responses, between 9 and 10 P.M. Thickness expressed as in Fig. 5. The circled point for cones in B is considered aberrant.

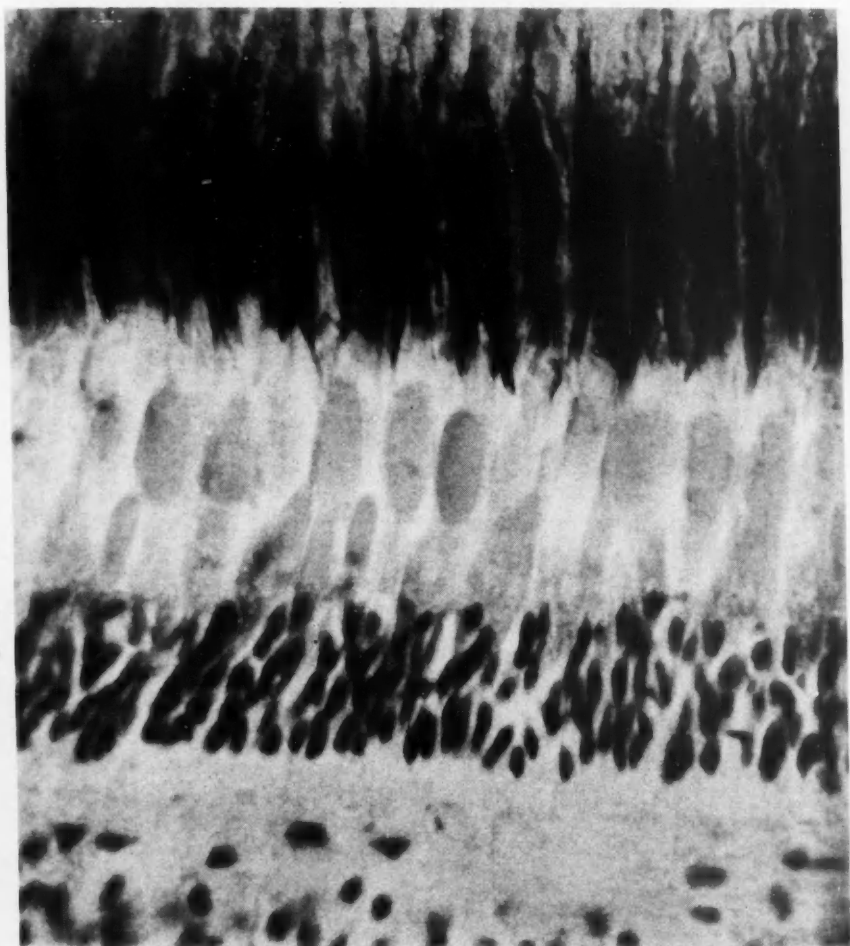


FIGURE 1. Light-adapted retina of a young coho, showing the pigment migrated into the finger-like processes of the pigmented epithelial layer, shielding the extended rods. The cones are in the advanced position with myoids fully contracted ($\times 500$, 3 min. Harris' haematoxylin and $\frac{1}{4}$ min. alcohol eosin).

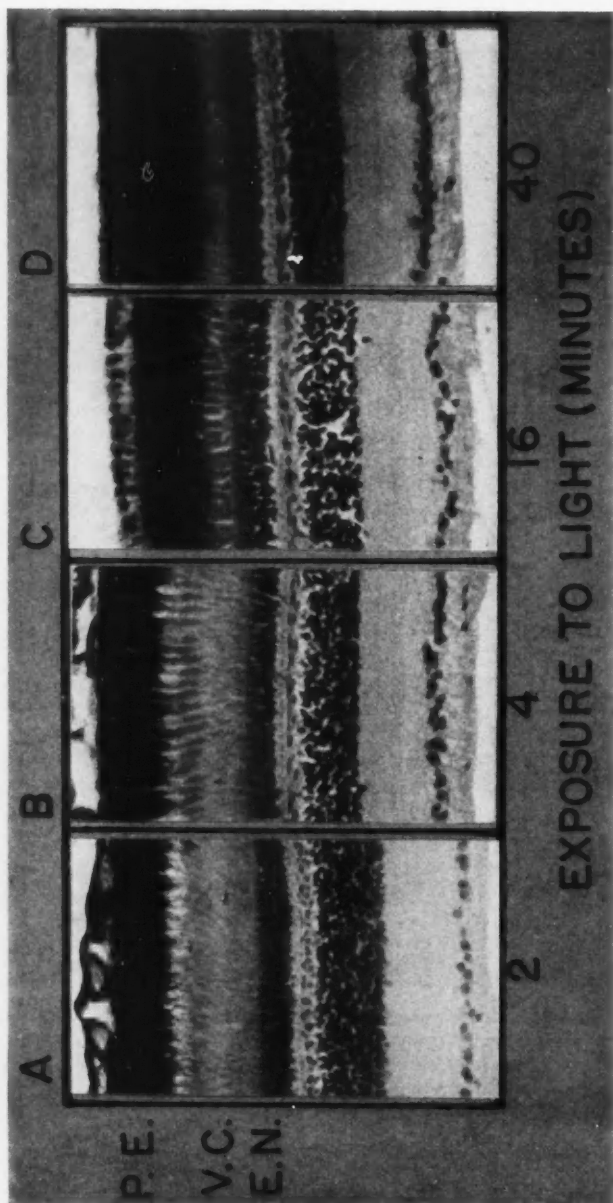


FIGURE 2. Photomicrographs showing four stages in the process of *light-adaptation* in young sockeye ($\times 20$). The external nuclear layers have been lined-up horizontally across the figure for ready comparison between sections from different eyes. Note how the pigment migrates into the visual cell layer, with greatest change between the 4 min. and 16 min. time intervals. It is also possible to see how the cones have contracted toward the external nuclear layer, advancing to receive the incoming light, while the rods have extended back into the shielding pigment of the epithelial layer. P.E., pigmented epithelial layer; V.C., visual cell layer; E.N., external nuclear layer.

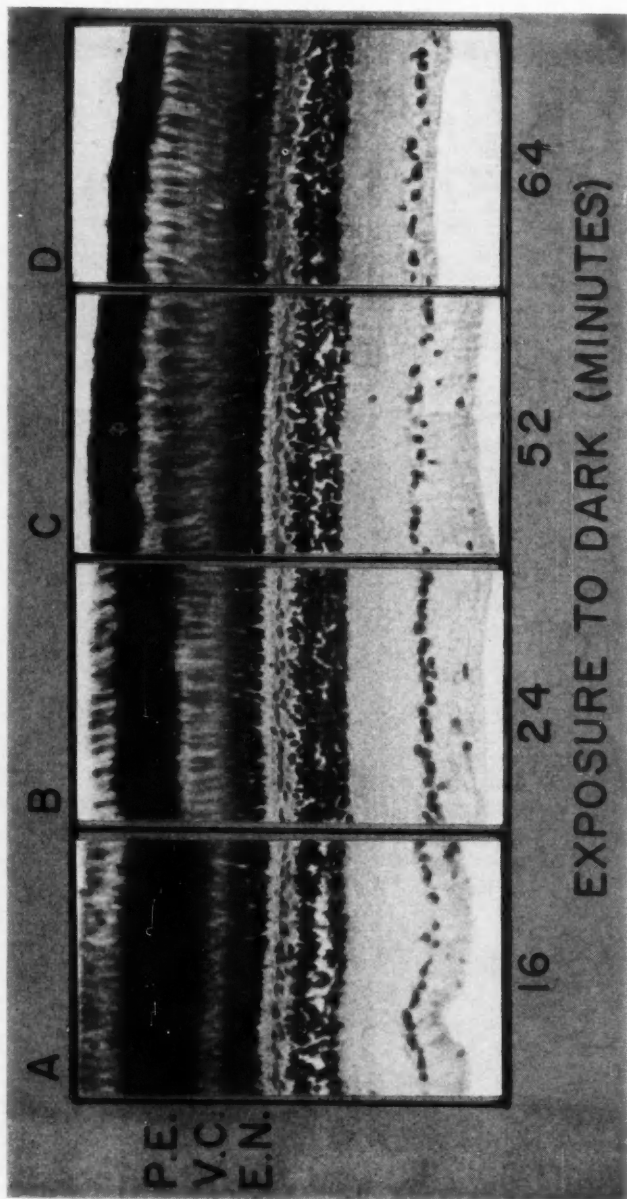


FIGURE 3. Photomicrographs showing four stages in the process of *dark-adaptation* in young sockeye ($\times 20$). There is little extension of the cones or movement of the pigment in the first 15 to 20 minutes in the dark, so that the 16-minute section shown here (A) is comparable with shorter exposure times. Note how dark-adaptation is a more gradual process in comparison with light-adaptation. Lettering as in Fig. 2.

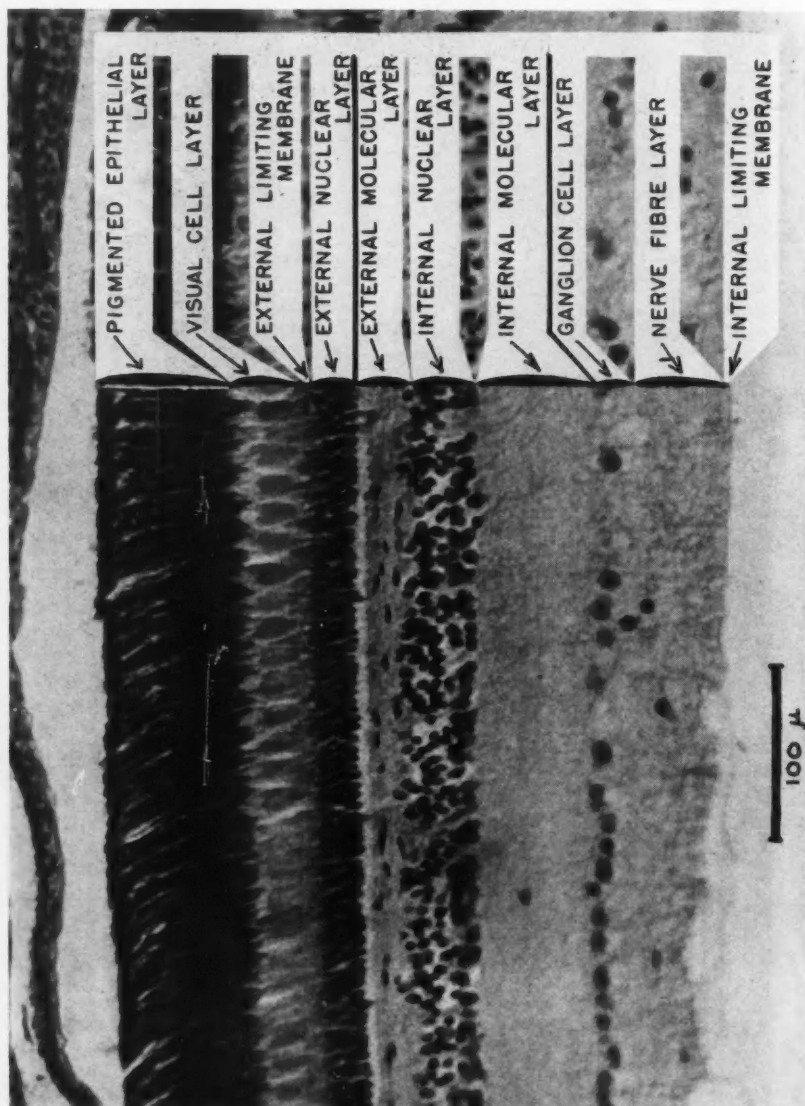


FIGURE 4. Photomicrograph of a light-adapted sockeye retina showing the 10 layers ($\times 200$). Stained as in Fig. 1.

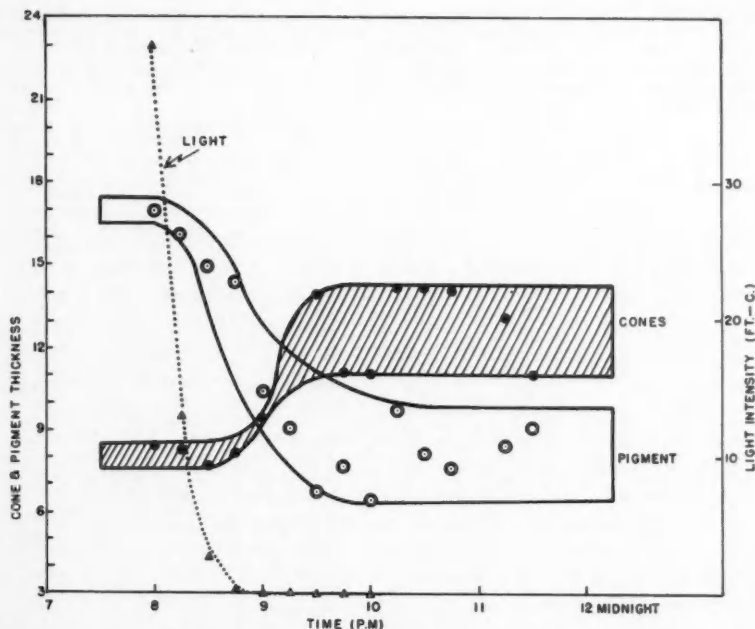


FIGURE 8. The rate of contraction of pigment and expansion of cones in pink fry sampled at Port John from an aquarium exposed to natural light. The decrease in the intensity of light at the time of sampling is shown.

of twin cones increases visual acuity. It is evident that twin cones are associated with surface-inhabiting forms exposed to bright light, for they decrease in numbers in deep-water fish and are absent altogether in nocturnal as well as really deep-sea fishes.

No *double* cones were observed in the *Oncorhynchus* eye, although they have been described in some teleosts like *Rutilus rutilus* (Greeff, 1900) *Fundulus heteroclitus* (Butcher, 1938), *Carassius auratus* (Walls, 1942) and particularly in the closely-related salmonids, *Salmo gairdneri irideus* and *S. trutta fario* (Verrier, 1935; McEwen, 1938). In addition there was no apparent variation in the number of cones in the different regions of the retina. However, the cones in the region of the fundus (which is often specialized for acuity) were larger than those in the peripheral region.

DIURNAL RHYTHMS. Diurnal variation in the movements of the pigment layer, rods and cones was not apparent in sockeye after they were constantly subjected to light or darkness for four days. No differences are apparent when the dark-adapted eye, fixed during the night, is compared with a light-adapted eye exposed to darkness for 128 minutes; likewise no difference is evident between a light-adapted eye fixed during the day and a dark-adapted eye exposed to light for 128 minutes.

TABLE II. Approximate time for different stages of dark-adaptation in migrating young salmon. Pink fry "held" were sampled from a shallow glass aquarium placed on top of the weir. Light intensities were taken in the same location, away from the shadow of trees. For specimens marked by an asterisk the stage of response was determined from inspection of retinæ, without confirmation by measurement, because of variability and small size of the sample; no samples were available before first time shown, because of nocturnal migration.

Species	Cell layer	Approximate timing and light intensity during photomechanical responses					
		Start		Halfway		Finish	
		Time	Intensity	Time	Intensity	Time	Intensity
		<i>P.M.</i>	<i>ft.-c.</i>	<i>P.M.</i>	<i>ft.-c.</i>	<i>P.M.</i>	<i>ft.-c.</i>
Sockeye (smolt)	Pigment	8:30	42	9:10	10	9:45	0.1
	Cone	8:45	22	9:10	10	9:45	0.1
	Rod	8:30	42	9:00	15	9:30	1.5
Coho (smolt)	Pigment	8:45	22	9:30	1.5	10:00	0.03
	Cone	9:0	15	9:45	0.1	10:15	0.01
	Rod	9:30	1.5	9:45	0.1	10:00	0.03
Pink (fry—held)	Pigment	8:15	13	8:45	0.5	9:45	0.00
	Cone	8:30	3	9:00	0.05	9:30	0.00
	Rod	8:30	3	9:00	0.05	9:30	0.00
Pink* (fry—migrant)	Pigment	9:15	0.01	9:45	0.00
	Cone	9:15	0.01	9:45	0.00
	Rod	9:15	0.01	9:45	0.00
Chum* (fry—migrant)	Pigment	9:30	0.00	10:00	0.00
	Cone	9:30	0.00	10:00	0.00
	Rod	9:30	0.00	10:00	0.00

Welsh and Osborne (1937) observed that a definite diurnal rhythm persisted in the dark-adapted eyes of *Ameiurus*. Under constant illumination, however, the rods and cones were found to remain constantly in the light-adapted state. Arey and Mundt (1941) noted that a diurnal rhythm existed with regard to the cones in *Ameiurus* kept in the dark, but found no satisfactory proof that this happened in the case of rods and pigment.

PHOTOMECHANICAL CHANGES. The photomechanical changes taking place in the vertebrate retina have been studied extensively by several authors and reviewed by Garten (1907), Arey (1915), Parker (1932) and Detwiler (1943). The most prominent changes recorded in the length of cones and rods occur in fishes (with the exception of the eel, Garten, 1907). As observed in *Oncorhynchus*, the cone and rod myoids may lengthen tenfold. Similar changes have been noted in other fishes like *Ameiurus* (Arey, 1928).

The process of contraction of the pigment layer is a much slower one than its expansion in light; similarly, the cones take a longer time to elongate in the dark than they do to contract in light. It would appear that when the eye is exposed to light, the pigment and cones respond quickly. The quicker response of the rods in darkness than in light is noteworthy and has been observed in the case of *Ameiurus* by Arey (1916).

DARK ADAPTATION DURING MIGRATION. The peak of evening migration in sockeye smolts usually occurs between the hours of 7 and 9 o'clock, as observed

in the Lakelse River run (see Fig. 12, Brett and Alderdice, 1958). The time of rapid increase in the number of migrants leaving the lake coincides with rapid changes in light intensity and to the onset of retinal responses culminating in dark-adaptation.

Young coho show greater diversity in time of daily migration, frequently moving in large numbers during mid-day. Neither species migrates during the dark hours between 1:00 A.M. and 4:00 A.M. Dark-adaptation in coho migrants appears to occur slightly later in the evening than in sockeye (Table II).

It is a characteristic of pink and chum fry, in the early stages of their migration, to seek cover under gravel or bottom debris, emerging after dark to swim actively downstream (Neave, 1955; Hoar, 1956). Even when released into an open impoundment at this stage they confine downstream movement to the period $1\frac{1}{2}$ hours after sunset to $1\frac{1}{2}$ hours before sunrise (MacKinnon and Brett, 1955). Unlike the diurnal smolt migrations, those of the fry are strictly nocturnal.

The first appearance of pink and chum fry in the counting weir at Port John, B.C. (located right on the fringe of the spawning grounds) was at approximately 9:15 and 9:30 P.M. respectively. These fish had undoubtedly just risen from the gravel. It is of interest to note that the pink fry held in an open aquarium showed about the same level of dark-adaptation as did the normal migrants. The latter, however, displayed greater variability, possibly indicative of the varying degree of cover obtained by individual migrants just prior to rising from the bottom. The stage of retinal response corresponding to the start of migration was that of approximately half dark-adapted.

Although no migratory timing mechanism can be concluded from the above relations, it is suggestive of a possible pathway which it would be of interest to test.

SUMMARY AND CONCLUSIONS

1. The retina of *Oncorhynchus* includes three types of visual cells, namely, rods, single cones and twin cones.
2. The large number of cones (18 ± 2 for $100 \mu^2$) and rods (14 ± 2 for $100 \mu^2$) indicate that the *Oncorhynchus* eye is adapted for vision in both bright and dim light.
3. In the light-adapted retina of *Oncorhynchus*, the cones were contracted to about 35μ , and the pigment layer and rods expanded to about 65μ each; in the dark-adapted condition, the cones were elongated to about $70-75 \mu$ and the pigment layer and the rods contracted to about $25-30 \mu$ and 30μ respectively.
4. Young sockeye were almost completely light-adapted in 20-25 minutes under laboratory conditions, and dark-adapted in 55-60 minutes.
5. Samples of sockeye and coho smolts from the Lakelse River were completely dark-adapted by 10:00 P.M., when the intensity at the surface was 0.03 ft.-c. The pink and chum fry sampled from the screen at Port John were dark-adapted by 9:45 P.M., when the intensity at the surface was less than 0.002 ft.-c.

6. Pink and chum fry rose from the gravel and commenced migrating downstream 15–30 minutes after the time when the eyes of free-swimming “control” fry had started to dark-adapt.

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Mortality Rates and Estimates of Theoretical Yield in Relation to Minimum Commercial Size of Lingcod (*Ophiodon elongatus*) from the Strait of Georgia, British Columbia¹

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ABSTRACT

Strap tags on the operculum of lingcod were recovered almost as frequently as celluloid rings around the upper jaw during their first year at large, but they were retaken much less frequently than celluloid tags in later years; after two years the rate of decrease in return of the two types of tags was about the same. For 1944-47, approximately, the total instantaneous rate of disappearance of tags from fish in the size range 66-90 cm. (56-85 cm. or ages 3-8 when tagged) was 0.46 for a combined calculation, and 0.43 as an average for individual calculations; corresponding apparent survival rates are 63% and 65%. Larger fish have a somewhat larger mortality rate; for smaller fish mortality cannot be measured because they are incompletely recruited. A survival rate for age 6-7, estimated from age and length composition, pertains to an earlier period (1935-40) and is somewhat larger (0.70). For the central range of sizes, instantaneous rate of fishing (1944-47) is estimated to lie between 0.15 and about 0.22, and instantaneous rate of natural mortality between 0.28 and 0.18, depending on what allowance should be made for non-return of tags and wandering of tagged fish. Graphs of yield against rate of fishing and minimum size limit indicate that the present limit (58 cm., 3 lb. dressed) permits greatest yield per age 1 recruit from the present rate of fishing. Increasing the rate of fishing, even when the size limit is adjusted to the best corresponding value, results in relatively small increases in equilibrium yield per age 1 recruit, and a relatively rapid decrease in yield per unit of effort.

INTRODUCTION

THE LINGCOD occurs in the continental shelf waters of the eastern Pacific Ocean from California to Alaska, with the centre of its geographic range and greatest apparent abundance in waters adjacent to British Columbia, Canada. The species is fished with trawls and lines. The latter are used for the most part in the sheltered waters of the Strait of Georgia, where a handline fishery of long standing is carried out from small vessels. Wilby (1937) gives a description of the species, and more details concerning distribution and fishing methods.

To obtain information on the growth, mortality and movements of lingcod, tagging experiments were begun in 1939 by the Fisheries Research Board of Canada. Chartered lingcod vessels were used, chiefly during closed seasons (December through February). A total of 2,465 handline-caught lingcod were tagged in the waters of the Strait of Georgia from 1939 through 1944, of which 65% were released in statistical areas 17 and 18 (Table I).

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Lingcod may attain an age of at least 15 years and may weigh 50 lbs. or more (Chatwin, 1956a). Recoveries of tags have shown that the lingcod undertakes no regular migrations, and is apparently quite sedentary in habit (Hart, 1943b; Chatwin, 1956b).

METHODS

TAGS USED AND TAGGING PROCEDURE. During the tagging period two types of tags were used and applied in different ways. In 1939 and 1940, monel metal or aluminum strap tags were clinched to the operculum or "cheek-bone" of the fish; 1,091 fish were tagged this way. For the 1941 to 1944 taggings, flat coils of red plastic (Hart, 1943a) were passed through a slit in the membrane between the upper jaw and the face, completely encircling the upper jaw bones (Fig. 1). In

TABLE I. Tags applied to line-caught lingcod in the Strait of Georgia, 1939-44. The Statistical Area or Areas in which each group was released is shown in brackets below the number. For the locations of these Areas, see figure 1 of Godfrey (1958), page 895 of this issue.

Year	Jan.	Feb.	March	April	May	Oct.	Nov.	Dec.	Total
1939	91 (17)	247 (14, 17, 18)	...	166 (17, 18)	...	98 (18, 20)	58 (17)	...	660
1940	224 (14, 17, 18)	78 (17, 18)	...	129 (13, 17)	431
1941	...	148 (17)	21 (18)	48 (17)	217
1942	64 (17, 18)	74 (17, 18)	...	172 (13)	9 (13)	319
1943	...	257 (17)	77 (17)	...	32 (17)	366
1944	74 (13)	398 (17)	472
1939-40	315	325	...	295	...	98	58	...	1091
1941-44	138	877	21	172	9	77	...	80	1374

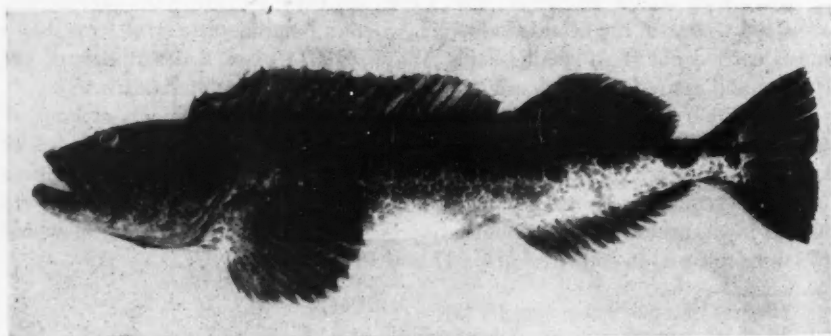


FIG. 1. A large lingcod, with tag attached to upper jaw. Length 106 cm.

addition to being more permanent, this tag is probably more conspicuous. Each coil comprised a little more than two complete turns. These tags were applied to 1,374 fish. Lingcod used for tagging and reported here were captured by handline, usually in 3 to 50 fathoms (5-90 m.) of water. Fish tagged were measured from the tip of the lower jaw with mouth closed to the end of the median rays of the tail, using a measuring board. The lingcod's tail is usually square, so that this is also the "total" length.

RECOVERIES. Tags from fish captured by a commercial fishery are, for various reasons, not always returned or made known to the agency concerned. In the case of lingcod the number of tags not returned is probably not too great, for the following reasons. During the late 1930's and early 1940's, concern was shown by the hand-line fishermen in the strait of Georgia regarding the perpetuation of the lingcod stocks. In the main, their apprehension stemmed from the increased demands placed on the lingcod stocks as a result of the increase in value of lingcod livers during that time. Accordingly, scientific investigations of the lingcod were begun. Direct contact with the fishery has been maintained since the tagging started, and a reward of \$1.00 has been offered for each tag returned accompanied by suitable recovery information. The interest in the experiments shown by most lingcod fishermen makes it unlikely that very many of them would intentionally refuse to return tags. Nevertheless there is certain to have been some forgetfulness and inadvertent loss³, and no good estimate can be made of its magnitude.

Failure to return all tags caught makes estimates of fishing rate too low, but estimates of *total* mortality rate are not affected if each recovery year had the same percentage non-return of tags.

Recoveries are grouped according to the number of days elapsed from the date of tagging, divided into periods a year long. For example, a fish tagged April 15, 1940, and recovered March 10, 1944, has been at large more than 3 but less than 4 full years, hence is assigned to year 4 of recovery.

TOTAL MORTALITY RATE. The rate of decrease in the numbers of tagged fish recaptured annually can be used to estimate total mortality rate of the stock provided that (1) tagged fish die and are caught at the same rate as untagged fish, and (2) fishing effort and catchability remain reasonably constant from year to year. Under these circumstances, when the base-10 logarithms of the number of recoveries are plotted against the year of recapture, they form a line with a negative slope. This slope, when antilogged, is the annual survival rate, s ; and

³ Dr. J. L. Hart tells the following anecdote. An interested Nanaimo fisherman had captured three tagged lingcod and, knowing that Dr. Hart preferred to see the fish whole when possible, held them alive for his personal examination. Wishing to preserve one or more tags *in situ*, Dr. Hart asked the fisherman to clean the fish and save the heads. With the skill and speed of long experience, the fisherman gutted the first fish, cut off the head, and automatically threw it overboard. A little embarrassed and apologetic, he proceeded to clean the second one, and did the same thing again! With the third fish, however, reflexes were brought under control and Dr. Hart obtained his specimen.

the slope multiplied by -2.303 is the instantaneous rate of mortality, i (Ricker, 1948, Section 4). Possible deviations from the conditions necessary for the use of this method are discussed below.

In addition, estimates of annual mortality have been made from the length distributions of the fish tagged, combined with information on rate of growth from vertebral studies (Chatwin, 1956a). Because the graph of length against age is approximately linear for only a few years, survival can be estimated by this method only in the middle of the range of uniform growth (Ricker, 1948, Section 10), which in this material is age 6 to age 7.

RATE OF FISHING. The instantaneous rate of fishing can be estimated from the graph of logarithms of recoveries against time, by extrapolating it back to time $t = \frac{1}{2}$, which is the beginning of the first recovery year—that is, the time of tagging. The antilogarithm of this intercept, divided by the number of fish tagged, is equal to $us^{-1/2}$, or the rate of exploitation divided by the square root of the survival rate; but when s is large, as in these experiments, it is for practical purposes equal to the instantaneous rate of fishing, p (*Ibid.*, Section 26).

Strictly, interpretation of the intercept in this manner would require a fishery of constant intensity throughout the year. The fishery actually is somewhat seasonal, heaviest catches being in March to May with a smaller peak in autumn, but trial calculations show that non-random distribution of fishing could change the estimated rate of fishing only in the third decimal place.

CATCH STATISTICS OF THE STRAIT OF GEORGIA LINGCOD FISHERY

The hand-line fishery for lingcod in British Columbia has a continuous history which goes back to aboriginal times. Reasonably good statistics for the commercial catch begin in 1927, but a complete breakdown by statistical areas is available only from 1950 (Table II). During the 1930's a few lingcod began to be

TABLE II. Total British Columbia catch of lingcod, and an estimate of the Strait of Georgia catch, in thousands of pounds. [The Strait of Georgia catch is estimated as 90% of the total catch in 1927-42; as 80% in 1943, 70% in 1944 and 1945, and 60% in 1946-49; in 1950, when regional statistics begin, it was 57%.]

Year	Total	Strait	Year	Total	Strait
1926	1941	4087	3700
1927	4992	4500	1942	4250	3800
1928	5077	4600	1943	5869	4700
1929	4849	4400	1944	8425	5900
1930	4859	4400	1945	7914	5500
1931	5099	4600	1946	7383	4400
1932	3996	3600	1947	3875	2300
1933	4028	3600	1948	6586	3900
1934	4781	4300	1949	7263	4300
1935	6284	5700	1950	4638	2506
1936	6893	6200	1951	4746	2134
1937	4286	3900	1952	4242	2452
1938	4652	4200	1953	2943	1705
1939	4750	4300	1954	3907	2281
1940	4761	4300	1955	3625	2201

taken by trawling, and during World War II this activity increased. Trawlers who concentrated on lingcod became adept at fishing close to the reefs, or part way up on the reefs, apparently scaring the fish out of their hiding places into the net. Some nets were lost, but the risk was compensated by the higher price per pound paid for lingcod as compared with other trawl species. However, it is likely that never more than 20% of the Strait of Georgia lingcod catch was taken by trawls (exact statistics are not available). In 1947 most of the traditional Strait of Georgia line-fishing grounds were closed to trawling, and since then the trawl catch has been only about 3% of the total for the Strait. The war also stimulated line fishing, both in the Strait of Georgia and outside. Catches reached a peak during 1944-46 and remained fairly high through 1949.

There are no direct statistics on fishing effort over the years, but the increased activity in wartime was very noticeable. Tagging done in 1939 and 1940 produced recaptures mainly from 1939 to 1942—a period of fairly stable catch averaging about 4,000,000 lb. in the Strait of Georgia. Tagging done in 1941-44 spans the period of increasing catch. However, since the number of tags put on in 1941 was rather small, while 1944 was the biggest year of the four, recoveries were mostly made during a period of rather high average fishing effort, 1942-49. The average catch during these years is estimated as about 4,300,000 lb., not much greater than the previous period, but because of the "fishing up" effect the increase in effort must have been relatively much greater. (This is because the yield from a fishery does not "settle down" to a level consonant with the prevailing rate of recruitment until some years after the stabilization of effort at a new level.) Although effort varied considerably between years within the period 1942-49, having the taggings spread over 4 years smooths out these variations and gives the combined data a stable and fairly representative character for that period.

RATE OF DECLINE OF TAG RECAPTURES

A total of 493 tagged lingcod have been recovered from these experiments (Tables III, IV).

Early returns from fish tagged with the opercular strap indicated that erosion of flesh and bone was occurring at the point of tag attachment, and this led to the adoption of the ring tag in 1941. Subsequently the recovery of 11.5% of strap tags and 26.8% of the ring tags indicated that the latter was a much superior tag for these fish. First-year recoveries were not greatly different (7.7% and 8.8%, respectively), but during later years far fewer strap tags were recovered.

Using, for reasons discussed below, only the central size groups from 66 to 95 cm., a general rate of decrease in tags available to the fishery can be estimated from the year-to-year decline of the two sorts:

Recovery year	1	2	3	4	5	6	7	8	9
Opercle tag	32	8	4	2	1	1	1	0	0
Jaw tag	63	39	33	14	9	1	2	2	3

Logarithms of these values are plotted in Figure 2. They are fitted with lines by weighted least squares—each value being weighted as the number of recoveries

TABLE III. Number of lingcod tagged using opercular strap tags in 1939-40, and numbers returned from recaptures made in successive 12-month periods following tag releases, arranged by 5-centimetre length intervals at time of tagging. The legal minimum size is 3 lb. dressed, head-off, or about 58 centimetres fork length.

Size-group	Number tagged	1	2	3	Year of recovery				unknown	Total
cm.					4	5	6	7		
36-40	3	0	1	no. %
41-45	7	1	1 33.3
46-50	52	1	1	1 14.3
51-55	135	8	1	2 3.8
56-60	189	13	4	1	1	1	9 6.7
61-65	219	20	8	0	0	1	1	20 10.6
66-70	145	16	1	1	0	1	30 13.7
71-75	96	6	3	1	0	0	0	1	...	19 13.1
76-80	56	4	2	1	2	11 11.5
81-85	52	3	1	0	0	0	1	9 16.1
86-90	30	2	1	1	5 9.6
91-95	29	1	4 13.3
96-100	25	2	3	1 3.4
101-105	21	4	1	5 20.0
106-110	17	2	5 23.8
111-115	4	1	2 }
116-120	7	1 }
127	1	0 }
unknown	3	0 }
Total	1091	84	27	5	3	3	1	1	1	125

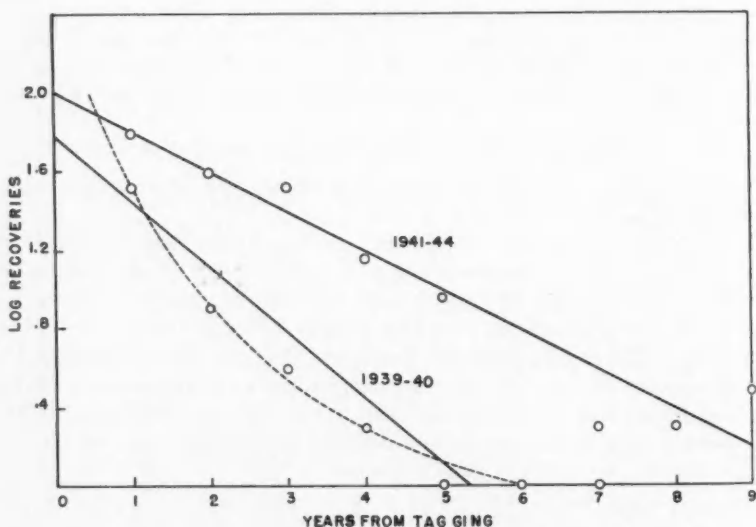


FIG. 2. Logarithms of the captures of lingcod 56-95 cm. long when tagged, arranged by years. Upper series: those tagged with jaw tags in 1941-44. Lower series: those tagged with opercle tags in 1939-40. (The point for year 6 applies to both series.) Straight lines are fitted by weighted least squares.

on which it is based. The apparent survival rates are 0.460 and 0.628, corresponding to apparent instantaneous mortality rates of 0.776 and 0.465.

The much more rapid disappearance of the strap tags is probably entirely a result of the shedding of the tags. The line of plot of log recaptures is, however, partly curved for the strap-tag series. From the 3rd to the 7th year it parallels the line for the jaw tags, and even the 2nd year point does not diverge significantly. This suggests that whatever tags are going to work loose mostly do so during the first, or at latest the second, year after tagging, the remainder staying firm from then on.

The ring tags on the jaw stayed firm without known exception—presumably because they were attached to a large strong bone, could not spring apart, and were made of material that seems indestructible within the period involved.

Assuming no actual loss from the jaw, the "other loss" of jaw tags, in the 1941–44 series, presumably consists largely of natural mortality. However, it can also include a rather insidious component which has been called the "going-away-factor". Fish populations, in general, live at different densities in different parts of their range; fishing tends to be concentrated on spots where fish are numerous per unit area, or easy to catch for any other reason. The fishing done for tagging, like regular commercial line fishing, was carried out mostly on reefs where lingcod are known to be abundant and available. After tagging, the cod were usually returned to the same place as they were caught, but the tag returns do indicate a certain amount of wandering done by this, for the most part, rather sedentary fish.⁴ This wandering presumably takes the fish, in part, into areas of lesser concentrations where they are less likely to be fished, and hence it makes them less vulnerable on the average, than when on their home grounds. Thus the rate of recapture has a tendency to be lower than it would otherwise be as long as wandering of fish away from the high-availability areas exceeds their rate of return to them. The chances are that after 2 or 3 years an equilibrium would be established between going-away and returning, and since these recoveries extend over a longer period than that, the slope of the lines in Fig. 2 and 3 should be only slightly affected. In later computations we have used 0.03 as a possible *net* instantaneous rate of leaving (excess of departures over returns).

CHANGE IN MORTALITY RATE WITH AGE

The young fish of a population become increasingly vulnerable to fishing during the period of "recruitment", which extends *at least* to the age most frequently represented in the catch. Beyond that point, however, there can still be changes in vulnerability with size. This has been examined in the returns from the 1941–44 tagging.

⁴ The fish which remain on favoured fishing grounds are more likely to be caught than those which stray, hence the percentage of distant recoveries is likely to underestimate the true amount of wandering.

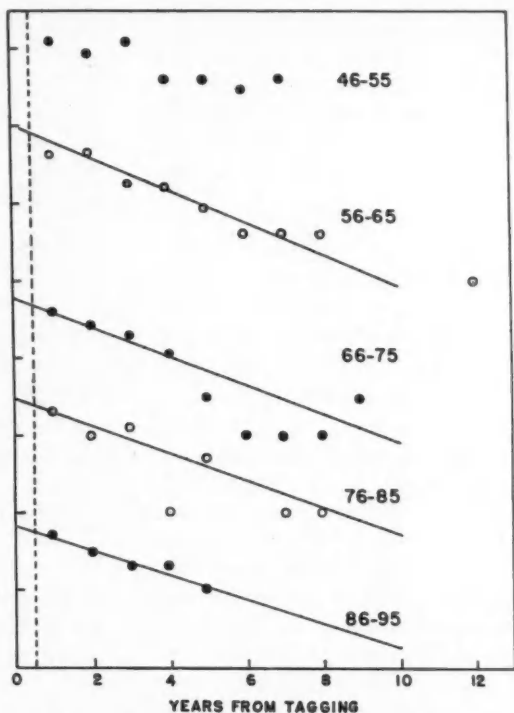


FIG. 3. Logarithms of returns of lingcod tags from the 1941-44 taggings, arranged by length at tagging and by year of recapture. Lines are fitted by weighted least squares (see text; original recapture date in Table IV).

Each length-group of fish in Table IV can be followed throughout its recapture history to see what changes in survival rate occur with increasing age. Unfortunately, for any one group the number of recaptures is so small that resulting estimates fluctuate widely. Combinations of fish of about the same age can be obtained, however, because over the length range 61-85 cm. the fish grow at an approximately uniform absolute rate, about 4.5 cm. per year, which is close to the 5-centimetre interval used in Table IV. Thus we can add recaptures along the appropriate parts of the NE-SW diagonals of the Table and so obtain a wider selection of fish of similar (not identical) length and age; these are then compared with the recaptures of the same group a year later. For example, along the diagonal starting at 71-75 cm. there are $15 + 18 + 8 + 7 = 48$ recaptures in the rows which start at age 3 or older, while such fish when a year older are represented by $8 + 12 + 9 + 6 = 35$ recaptures. The full series and derived apparent survival rates are given in Table V.

TABLE V. Recoveries of 1941-44 tags arranged in groups approximately uniform as to average age, by adding parts of the diagonal series of Table IV (see text).

Approximate size range when tagged	Average age during 1st year of recovery	1st year recoveries	2nd year recoveries	Apparent survival rate	Apparent instantaneous mortality rate
cm.	years	no.	no.	s'	i'
56-60	3.8	23	20	0.869	0.140
61-65	4.5	41	37	0.902	0.103
66-70	5.5	60	33	0.550	0.599
71-75	6.5	48	35	0.729	0.316
76-80	7.5	45	27	0.600	0.511
81-85	8.5	37	22	0.594	0.521
86+	9.5+	64	36	0.562	0.576

The fish averaging 5.5 years and older during the first recovery year can provisionally be considered "fully recruited", and hence their apparent survival rates may be estimates of true survival. The average survival rate for ages 5.5 to 7.5 is 95/153 or 62%; the corresponding instantaneous mortality rate is 0.476. The decrease of survival to 56% among older fish is probably real, and a reflection of gradually increasing senility. Another evidence of an increased natural mortality rate among old fish is the gradual disappearance of males, the oldest individuals being nearly all female.

Fish 4.5 years and younger in their first recapture year show higher apparent survivals than the next older age groups. However it is impossible to apportion this accurately between two causes: an "artificial" reduction in apparent mortality resulting from the fact that rate of exploitation is increasing with age (Ricker, 1948, Section 27), and a true tendency for total mortality rate to be smaller because relatively fewer of the smaller fish are caught. If some assumption be made concerning the magnitude of the natural mortality rate during years of recruitment, values of p can be estimated from the tag returns (*Ibid.*, table 11). However, with these lingcod the "other loss" is apparently of the same order as the rate of tag return, and there is a good chance that the natural death rate may increase among the smaller fish as a result of (known) cannibalism by the larger ones. Thus it is unlikely that a calculation of this kind would give a useful result.

For our purpose, the principal importance of the data of Table V is that the apparent survival rate does not vary significantly with age or size from 66 cm. on up, except that the decline among the scarce big fish is probably real.

RATE OF TAG RETURN AND RATE OF FISHING

RATE OF RETURN OF TAGS. A distinction will be made between rate of fishing (p) and rate of return of tags (p'), the difference being the rate of failure to turn in tags actually captured. An estimate of rate of tag return (p') for the 552 fish tagged in the central size range (66-95 cm.) can be made from Fig. 2. For the 1941-44 tags, the intercept of the line of fit at $t = 0.5$ is 1.914, whose antilogarithm is 82, so that the instantaneous rate of tag return is estimated as $p' = 82/552 = 0.148$.

Loss of tags from the fish makes similar estimates for the 408 intermediate-size fish of the 1939-1940 tagging much less certain. If the points of Fig. 2 could be considered acceptably straight, an extrapolation similar to the above gives 1.625, antilog 42, hence $p' = 42/408 = 0.103$. However the line is almost certainly curved; an attempt at freehand curvilinear extrapolation to $t = 0.5$ gives 1.95, antilog 89, $p' = 89/408 = 0.22$, but naturally little weight can be attached to such an estimate.

RATE OF TAG RETURN BY SIZE. Rate of return of tags was also estimated by the method of Fig. 2 for a series of 10-cm. size groups of the 1941-44 tagging, as shown in Fig. 3 and Table VI. There is no convincing evidence of any change in rate with size, though the slightly higher rate for the 56-65 cm. group may not be entirely artificial. An average value for p' would be 0.15, in agreement with the combined calculation for the 66-95 cm. range, made above.

TABLE VI. Estimates of survival rate and the instantaneous rates of total mortality, fishing and natural mortality, estimated for four size groups of tagged fish. (Natural and total mortality may include some effect of "going-away". The first-year recoveries were not used in estimating i' and p' for the 56-65 cm. group; this slightly over-corrects for their incomplete vulnerability in the first year, so the estimated p' tends to be high and q' low.)

Size when tagged	No. tagged	Total recaptures	Survival rate	Total mortality	Rate of tag return	Apparent natural mortality
cm.			s'	i'	p'	q'
56-65	498	147	0.618	0.481	0.170-	0.311+
66-75	338	103	0.651	0.430	0.142	0.288
76-85	158	50	0.668	0.402	0.153	0.249
86-95	56	13	0.697	0.359	0.101	0.258

The rates of total disappearance, i' , for these separate graphs are consistently a little lower than the figure 0.46 obtained from Fig. 2, so the "other-loss" (apparent natural mortality, q') rates are also lower. An average value for the latter is about 0.28, as compared with 0.31 from the combined calculation.

ADJUSTMENT FOR FAILURE TO RETURN TAGS. Failure to report tags actually recaptured makes p' smaller than true rate of fishing, p , and q' larger than true rate of natural mortality, q . Unfortunately, any correction for this effect is only a guess. If the true recapture rate be taken as $\frac{1}{2}$ greater than the rate of return of tags, p' is increased to $p = 0.22$ and q' is reduced to 0.21, i' remaining unaffected. This is probably somewhat too great an adjustment upward for p , but not an impossible one.

ADJUSTMENT FOR THE "GOING-AWAY FACTOR". Any excess of movement of tagged fish to less vulnerable localities will make for a larger "total loss" rate, i' . For example, if this effect made i' 0.03 greater than the true total mortality rate, i , the q' values above should also be reduced by that amount to indicate true mortality rate, q , while p values are not changed.

RATE OF FISHING AND RATE OF NATURAL MORTALITY. A schedule of possible instantaneous rates of fishing and natural mortality, on the above basis, is shown below:

	Adjustment for "going-away"	
	None	0.03
Rate of fishing, p		
Minimum	.15	.15
With adjustment for non-return	.22	.22
Rate of natural mortality, q		
Maximum	.28	.25
With adjustment for non-return	.21	.18
Total mortality rate, i		
Observed	.43	.40

A best guess concerning the true rates might be $p = 0.20$, $q = 0.20$, $i = 0.40$.

SURVIVAL ESTIMATED FROM LENGTH FREQUENCY DISTRIBUTION AND RATE OF GROWTH

An independent estimate of rate of survival can be made for fish of medium size, though it applies to an earlier time than that from tag return. Chatwin (1956a) has estimated the age of Strait of Georgia lingcod from vertebral markings, and shows that the rate of growth obtained agrees quite well with the observed increase in length of tagged fish. From age 5 to age 8 growth is almost at a uniform absolute rate per year, the average for the two sexes being 4.5 cm. per year. Assuming that fish of these sizes are randomly sampled by the hand-line fishing which took fish for tagging, the corresponding frequencies for age 6-7 in Tables III and IV can be used to estimate survival rate. The points showing log frequency against size are plotted in Fig. 4. The curves are fitted by eye. Their slope provides an estimate of survival rate only in the middle of the range of uniform absolute increase in length—that is, age 6-7; also, this estimate applies to the median time of recruitment (at ages 2-3) of the year-classes in question, or approximately 4 years earlier than the mean date the samples were taken (Ricker, 1948, Section 8).

For both curves, the difference of logarithm from approximately age 6 to age 7 is -0.17 for 5 cm. of length. To convert to years, this is multiplied by 4.5/5, giving -0.153, of which the antilogarithm is an estimate of the yearly survival rate, $s = 0.70$. This applies to fish of age 6-7 at a time 4 years previous to the collection of the samples, that is 1935-36 for the one curve and 1937-40 for the other.

Although it has the same slope between age 6 and age 7, the curve for 1939-40 in Fig. 4 differs from the 1941-44 curve in being less steep at the older ages. This outer portion, beyond 80 cm., must reflect an earlier period of less mortality and greater survival rate, though unfortunately it is not possible to calculate actual survival rates at such sizes because of the decreasing rate of

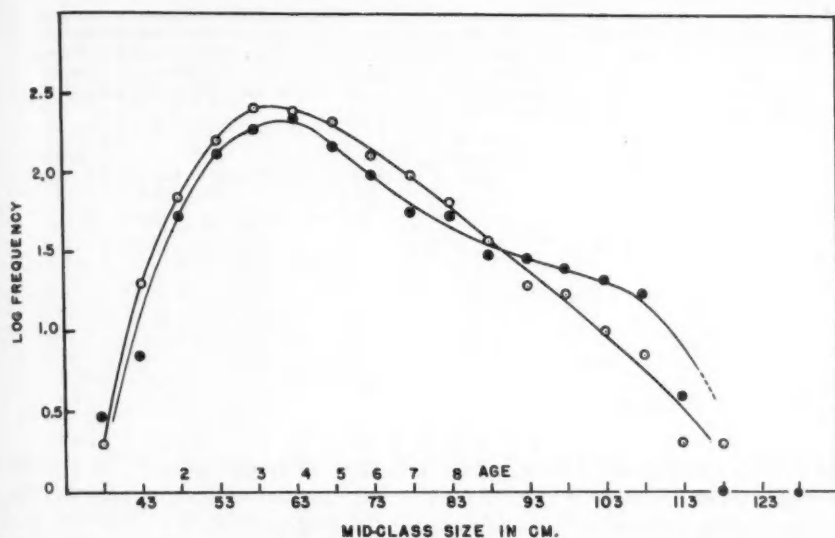


FIG. 4. Logarithms of length frequencies of lingcod used for tagging, with approximate corresponding ages shown on the abscissa.

growth in length. The statistics of Table II indicate somewhat lower than average catches in 1932 and 1933, which would lie within the period described by the flatter outer portion of the 1939-40 curve.

The age 6-7 mortality rates estimated by the two methods are compared below:

Method	Sample years	Principal survival years	Apparent survival rate (age 6-7)	Apparent instantaneous mortality rate
Length frequencies	1941-44	1935-40	0.70	0.35
Tag recaptures	1942-54	1944-47	0.63-0.65	0.43-0.46

The increase in mortality is presumably a direct result of the wartime increase in rate of fishing, p , after deducting any allowance needed for a "going-away-factor" in the estimate from tag recaptures. Allowing say 0.03 for this effect, the increase in p is 0.05-0.08 from 1938 to 1946 (median years); without any such allowance, the increase in p is 0.08-0.11 over the same period.

YIELD IN RELATION TO MINIMUM SIZE AND RATE OF FISHING

The present minimum legal size of 3 lb. dressed weight corresponds to 58 cm. (23 in.) fork length, hence permits the capture of most lingcod of age 4 and a substantial majority of those of age 3 (Table VII). In order to examine the effect, upon yield, of a smaller or a larger size limit applied to any given weight

TABLE VII. Average fork length and round weight of male and female lingcod in the Strait of Georgia, and approximate instantaneous growth rates (g). (Figures shown are averages of the computed lengths and weights of males and females of each age, without adjustment for excess of females at the older ages. The growth rates are equal to the difference of the natural logarithms of adjacent weights, smoothed graphically beyond age 5. The growth rate shown opposite a given age applies to the year just completed.)

Age ^a	Length	Weight	Growth rate	Age	Length	Weight	Growth rate
<i>yr.</i>	<i>mm.</i>	<i>lb.</i>			<i>mm.</i>	<i>lb.</i>	
1	295	0.38	...	8	825	12.78	0.16
2	465	1.81	1.56	9	860	14.7	0.14
3	565	3.51	0.66	10	890	16.5	0.12
4	635	5.24	0.40	11	920	18.5	0.10
5	693	7.02	0.29	12	942	20.1	0.09
6	737	8.68	0.24	13	968	22.1	0.08
7	780	10.54	0.20	14	985	23.6	0.07

^aIn years just completed.

of recruits entering the fishery, equilibrium yield computations have been made in the manner described by Ricker (1945), but using an arithmetic mean for the average stock on hand each year (Ricker, 1958, Section 10C).

The observed situation (for the middle 1940's) is examined first (Table VIII, IX). Because of the uncertainty regarding what share of the total mortality rate should be ascribed to fishing and what to natural mortality, three different combinations of fishing and of natural mortality are used for the central range of ages: $p = 0.15$ with $q = 0.25$, $p = 0.20$ with $q = 0.20$, and $p = 0.25$ with $q = 0.15$, the total being 0.40 in each case (Table IX, columns 4-6). The natural mortality rate is increased slightly at ages less than 4, and is increased at an accelerating rate at ages greater than 10, as shown in Table VIII.

EFFECT OF CHANGING THE MINIMUM SIZE LIMIT. The figures for minimum age 3 in columns 4-6 of Table IX represent the yield per pound of age 1 fish, for the present size limit (approximately) and for three possible combinations of p and q which are consistent with our data. Naturally, since $p + q$ is constant, column 7 indicates a larger yield than column 6, and column 5 indicates a smaller yield than column 6. This is true regardless of what minimum size limit is in effect. However, the minimum limit for which the estimated yield is a maximum varies: it is least for $p = 0.15$ and $q = 0.25$, where it falls at about 50 cm., between age 2 and age 3; and it is greatest for $p = 0.25$ and $q = 0.15$, where it falls at about 68 cm., between ages 4 and 5. For $p = 0.20$ and $q = 0.20$ the best minimum size is at age 3.4 years and 60 cm., or very slightly larger than the present limit.

Thus the uncertainty regarding the percentage return of recaptured tags leads directly to uncertainty concerning the best minimum size. If our "best guess" of $p = 0.20$ and $q = 0.20$ is valid, the present minimum size of 58 cm. provides very close to the maximum catch with the present fishing effort—for any fixed level of reproduction.

TABLE VIII. Example of a computation of equilibrium yield, for a rate of fishing (p) of 0.2, and for an instantaneous rate of natural mortality (q) equal to 0.2 in the central range of ages, and increasing as shown among older and younger fish. The instantaneous rate of growth (g) is from Table VII. From the net instantaneous rate of change (column 5) the change factor (column 6) is obtained from Appendix II, and the corresponding stock change is found by successive multiplication in column 7. Column 8 is the arithmetic mean of adjacent values in column 7, and these multiplied by p give the yield in column 9. Columns 10-14 show the computation of yield for successively larger minimum age limits. Column 10 gives the net instantaneous rate of increase in the absence of fishing, with the corresponding change factors in column 11 and corresponding stock sizes in column 12. Column 13 is the total yield (sum of column 9) as it would be reduced by an immediate loss of the fish of the age-group shown at the left plus all younger ages. That is, the first entry is $433.06 - 37.46 = 395.60$; the second is $433.06 - 37.46 - 59.69 = 335.91$, etc. In column 14 these "reduced" yields are multiplied by the ratio of stock size in column 12 to stock size in column 7, in order to obtain the equilibrium yield from the whole stock when the age-groups fished exclude those above the line in question. That is, the yield is $395.60 \times 335.4/274.6 = 483$ lb. when age 2 and older are vulnerable, 501 lb. when age 3 and older are vulnerable, etc.

Age interval	p	q	g	$g-p-q$	Factor	Stock	Mean stock	Yield	$g-q$	Factor	Stock	"Reduced" yield	New yield
yr.						lb.	lb.	lb.			lb.	lb.	lb.
1-2	.2	.35	1.56	+1.01	2.746	100	187.3	37.46	+1.21	3.354	100	395.60	483.19
2-3	.2	.3	.66	+0.16	1.174	274.6	208.49	59.69	+0.36	1.433	335.4	335.91	500.80
3-4	.2	.25	.40	-0.05	0.951	322.38	314.48	62.89	+0.15	1.162	480.63	273.02	497.35
4-5	.2	.2	.29	-0.11	0.896	306.58	290.64	58.13	+0.09	1.094	558.49	214.89	477.96
5-6	.2	.2	.24	-0.16	0.852	274.70	254.37	50.87	+0.04	1.0408	610.99	164.02	445.66
6-7	.2	.2	.20	-0.20	0.819	234.04	212.86	42.57	0	1.0000	635.92	121.45	402.92
7-8	.2	.2	.16	-0.24	0.787	191.08	171.26	34.25	-0.04	0.9608	635.92	87.20	353.19
8-9	.2	.2	.14	-0.26	0.771	150.85	133.58	26.72	-0.06	0.9418	610.99	60.48	296.22
9-10	.2	.2	.12	-0.28	0.756	116.31	102.12	20.42	-0.08		575.43		
10-11	.2	.25	.10	-0.35	0.705	87.93	74.96	14.99	-0.15				
11-12	.2	.3	.09	-0.41	0.664	62.00	51.57	10.31	-0.21				
12-13	.2	.35	.08	-0.47	0.625	41.16	33.44	6.68	-0.27				
13-14	.2	.4	.07	-0.52	0.589	25.73	20.44	4.08	-0.32				
14-15	.2	.5	.06	-0.64	0.527	15.15	11.57	2.31	-0.44				
15-16	.2	.6	.05	-0.75	0.472	7.98	5.88	1.17	-0.55				
16-17	.2	.8	.04	-0.96	0.383	3.77	2.61	0.62	-0.76				
Total						1.44		433.06					

TABLE IX. Calculated equilibrium yield of the lingcod fishery, in pounds round weight per 100 lb. of fish entering age 1, for different values of rate of fishing, p , and natural mortality, q . (The rate of fishing, p , is the same at all ages; q has the indicated value at the central ages 5-9, but it increases at older and younger ages by the same absolute amount in all computations, the actual values when central $q = 0.2$ being shown in Table VIII.) In columns 4-6 total mortality is constant at $i = 0.4$ (in the central ages). In columns 7-11, $q = 0.2$ for central ages, and this is combined with five different values of rate of fishing, p .

1	2	3	4	5	6	7	8	9	10	11
Fish at recruitment			Yield in pounds per 100 lb. of fish reaching age 1							
Age	Av. length	Av. weight	p .15 q .25	.20	.25 .15	.10 .20	.20	.30 .20	.40 .20	.50 .20
yr.	mm.	g.								
1	295	0.38	325	433	541	356	433	430	407	376
2	465	1.81	345	483	633	373	483	510	510	503
3	565	3.51	340	501	693	367	501	548	567	572
4	635	5.24	322	497	724	352	497	560	589	604
5	693	7.02	293	478	731	327	478	540	589	613
6	737	8.68	261	446	716	296	446	524	571	599
7	780	10.54	224	403	680	260	403	484	533	568
8	825	12.78	186	353	627	222	353	433	484	520
9	860	14.7	151	299	558	183	299	374	425	462

CHANGE IN RATE OF FISHING. The effects of changing rate of fishing are examined in columns 8-12 of Table IX. Yield is plotted against minimum size in Fig. 5, while Fig. 6 is a Beverton-Holt type isopleth diagram. A decrease from $p = 0.2$ to $p = 0.1$ decreases equilibrium yield at all minimum sizes (Fig. 5), although of course not proportionately. An increase from $p = 0.2$ to $p = 0.3$ increases catch (except with the smallest minimum size limit, shown where the 0.1 and 0.2 lines cross). However, the increase is at best only moderate: the *greatest* absolute distance between the 0.2 and 0.3 lines in Fig. 5 is 80 lb., which is about a 20% increase at the minimum size where it occurs. Further increases in p produce further increases in catch when combined with the higher size limits, but these increases rapidly become smaller, as shown by the decreasing distances between the p lines in Fig. 5.

Assuming the physical effort and expense of fishing to be proportional to p , the fishermen obtain a 38% increase in catch for doubling their effective effort to raise p from 0.1 to 0.2 (at the present minimum size). Another equal increase in effort and rate of fishing, from the present 0.2 to 0.3, increases catch only by an additional 14% (of the $p = 0.1$ figure). Obviously, an economic limit to possible increase in effort would very soon be reached, if it has not been reached already. Conversely, a decrease in rate of fishing to $p = 0.1$, which is half the estimated present level, would reduce yield by 28% while *increasing* catch per unit of effort by 45%—but this would require a reduction of the fishing fleet to approximately half its present size.

According to Fig. 5 and 6, increase in effort would give somewhat larger yields if the minimum size limit were raised at the same time. It happens, however, that the present 58-cm. limit (3 lb. dressed) is so situated that changes in it have relatively small effects, whether fishing is increased or whether it is decreased. This is because on each curve of Fig. 5 the 58 cm. intercept is not

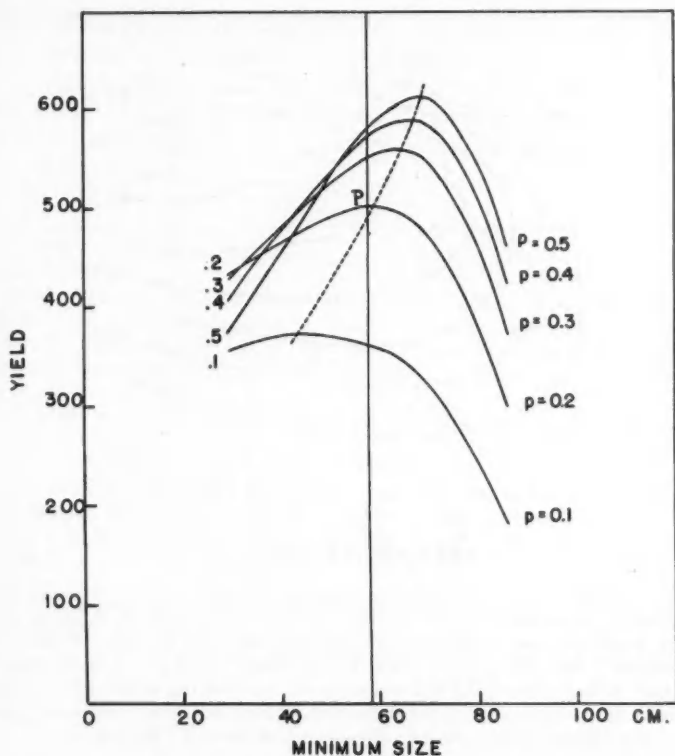


FIG. 5. Equilibrium yield of lingcod for different minimum size limits (on abscissa) and different rates of fishing, p , when the instantaneous rate of natural mortality is 0.2 in the central range of sizes. Yields, on the ordinate, are in pounds per 100 lb. of fish at age 1. The vertical line at 58 cm. marks the present minimum size limit. The best estimate of present conditions is the intersection of this line with the curve for $p = 0.2$, marked "P". Domes of the yield curves are joined by the broken line of "eumetric" fishing. Data from Table IX.

too far from the dome, in vertical distance. For example, increasing p from 0.2 to 0.3, without change in minimum size, increases equilibrium yield by 10%; if the minimum is raised to 63 cm. this is further raised to only about 11.5%.

OTHER COMBINATIONS OF FISHING AND NATURAL MORTALITY. The above discussions start from the basis of the equal division of total mortality between fishing and natural causes shown in column 5 of Table IX. Relationships similar to those shown in Fig. 5 and 6 can be computed also on the basis of the other two $p:q$ ratios, shown in columns 4 and 6, respectively, of Table IX. These are not reproduced here, but in general shape they resemble Fig. 5 and 6. With the

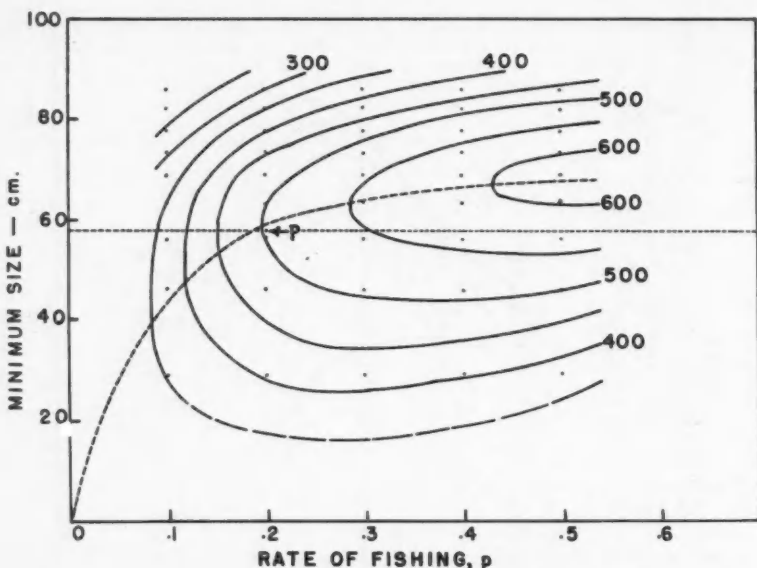


FIG. 6. A Beverton-Holt type isopleth diagram, showing contours of equal yield corresponding to minimum sizes on the ordinate and to rates of fishing on the abscissa. Isopleths were interpolated freehand using the data of Table IX plotted at the positions indicated by small dots. The ascending broken curve is the line of "eumetric" fishing, showing the best minimum size for each rate of fishing. The point "P" marks the best estimate of the present conditions, along the horizontal broken line representing the present minimum size of 58 cm. (3 lb. dressed).

larger natural mortality rate (central $q = 0.25$, column 4, Table IX) the yields for a given p are of course considerably less, while for central $q = 0.15$ they are much greater. The minimum size which gives maximum yield (for a given p) is somewhat less with $q = 0.25$, and somewhat greater with $q = 0.15$. However, general *relative* positions of the yield lines do not change a great deal.

CONCLUSION. The general conclusion must be that no manipulation of size limit, and no combination of size limit with any rate of fishing that now seems economic, could substantially increase this lingcod fishery's yield per unit weight of age 1 fish available. Unfortunately nothing is known, as yet, concerning the effect of the fishery upon rate of recruitment or rate of growth, either of which might be a more important factor in determining equilibrium yield.

ACKNOWLEDGMENTS

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the design of the superior tag used after 1940. Success of the investigation is the result of the co-operation of many lingcod fishermen, and others who assisted with tagging operations and in the return of tags. Assistance in tabulation and analysis of the data was given by Messrs. C. R. Forrester, K. S. Ketchen and W. E. Ricker, and the last-named collaborated in the preparation of the final draft of the manuscript.

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Progress Report of Drift Bottle Releases in the Northeast Pacific Ocean¹

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ABSTRACT

Twenty-five thousand drift bottles have been released in lots of one thousand at Ocean Weather Station PAPA and at eleven selected positions in the northeast Pacific Ocean. To April 15, 1958, there have been 816 returns.

The principal characteristics of the surface movement, as shown by the drift bottle paths, are in agreement with the geopotential topography, allowing for a component of movement generally to the right across the isobars. The drift bottle results substantiate the seasonal changes in surface movement implied by the geopotential topography. They also show the changes that occur between the periods of the oceanographic surveys.

Frequency distribution curves, used to determine the "most probable time at sea" of the drift bottles were similar for all releases.

The "most probable speeds" varied between 3 and 9 miles per day and are comparable to average speeds calculated from the geopotential topography.

INTRODUCTION

FOLLOWING PROJECT NORPAC (Dodimead, 1956) in 1955, a program was undertaken to study the oceanography of the northeast Pacific Ocean. It was designed to define the principal oceanographic features in this area, and to determine their seasonal and yearly variations.

As an aid in the study of surface currents, drift bottle releases were initiated in August 1956 and will continue at least until August 1958. There are now sufficient returns to warrant a study of the releases made prior to December 1957.

DRIFT BOTTLES

The drift bottles are 12-ounce, brown, Canadian beer bottles containing a card indicating the information required (Fig. 1). They were sealed with a cork and the necks dipped in "waterworks" tar, and packaged in cardboard cartons of 50 (later 24). The bottles were released in lots of 1,000 by breaking the tape-seal on the carton and dropping the case and contents overboard. The carton soon broke up, especially in a slight sea, and released the bottles, which floated on their sides.

In the planning of this project, it was reasoned that in view of the sparse and scattered population in the regions of anticipated returns it should be undertaken boldly or not at all. It was estimated on the basis of experience elsewhere that the returns would be between 3 and 5%. Therefore the releases had to be large enough for such returns to be statistically significant. To ensure even this level of return there had to be sufficient incentive in the reward to encourage search of the beaches. These objects were accomplished by releasing such a large number (1,000) bottles at a time, and making the reward one dollar.

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TABLE I. Description of drift bottle releases.

No.	Position of release	Date of release	No. of returns	Probable days at sea	Percentage returns to April 15, 1958	Speed in miles per day	
1	Ocean Weather Station "PAPA" (Lat. 50° 00' N., Long. 145° 00' W.)	Aug. 25/56	106	303	10.6	3.2	
2		Sept. 29/56	79	216	7.9	3.3	
3		Nov. 2/56	61	204 ¹	6.1	3.8	
4		Dec. 18/56	—	236 ²	—	5.6	
5		Jan. 25/57	20	231	2.0	5.2	
6		Mar. 9/57	28	307	2.8	3.7	
7		Apr. 19/57	22	162	2.2	4.1	
8		May 31/57	7	...	0.7	...	
9		July 12/57	4	...	0.4	...	
10		Aug. 24/57	7	...	0.7	...	
11		Sept. 27/57	22	106 ³	2.2	9.2	
12		Nov. 2/57	—	180 ⁴	—	6.7	
				115	6.6	6.8	
			4	...	0.4	...	
			426				
Survey Releases							
	N.	W.					
13	53° 10';	156° 46'	Aug. 23/56	39	250	3.9	5.4
14	48° 25';	152° 11'	Aug. 25/56	111	303	11.1	4.1
15	44° 49';	148° 56'	Aug. 26/56	1	544	0.1	5.0
16	40° 00';	145° 00'	Aug. 27/56	0	...	0	...
17	52° 55';	160° 37'	Feb. 5/57	7	...	0.7	...
18	45° 40';	154° 34'	Feb. 8/57	160	323	16.0	3.9
19	55° 35';	142° 40'	Feb. 17/57	47	123 ⁵	4.7	3.7
					185 ⁵	—	5.2
20	41° 45';	140° 37'	Feb. 28/57	0	—	0	—
21	53° 00';	156° 02'	Aug. 4/57	11	210	1.1	3.0
22	45° 22';	153° 55'	Aug. 7/57	10	191	1.0	8.5
23	55° 43';	142° 21'	Aug. 17/57	4	...	0.4	...
				390			

¹Returns from region between 130°–140° W. longitude.²Returns from region between 150°–160° W. longitude.³Returns from Middleton Island, Gulf of Alaska.⁴Returns from Kodiak Island, Gulf of Alaska.⁵Returns from region between 160°–170° W. longitude.

far westward as the end of the Aleutian chain (long. 175°E.). One bottle was returned from the Pribiloff Islands in the Bering Sea. There have been only three returns from south of lat. 42°N., two from the southern coast of California, and one from the Hawaiian Islands.

The greatest number of returns from any one release has come from south of Juan de Fuca Strait (lat. 48°N.). The beaches are generally sandy in this region and it is well populated. Northward of Juan de Fuca Strait along the ocean coast the shoreline is generally rocky and "steep to" with small beaches at infrequent intervals. The population is sparse, with only small settlements located several miles inland, in the sheltered inlets or harbours. People visit the ocean beaches digging for clams or for pleasure and exercise. The recovery of the drift bottles depends upon such occasional activity.

It is significant that 5 to 20 recoveries are made at one time by one or a few persons from one locality. Presumably one bottle is found by chance, then

spurred by the incentive of the reward, a thorough search of the local shore is made. There is no doubt that there are many bottles still on the unfrequented beaches.

The returns from each release were received from people living in separate settlements scattered along 100 to 500 miles of the coast. It is probable that these represent the greatest concentration of the landing from one release. It is probable that a closer search of the beaches would reveal a diminishing frequency of landing in neighbouring sections of the coast.

The proportion of returns from the North American coast has usually reached 4 to 16% within one year of release. This must be regarded as significant. When returns are received after one year it may be suspected that the bottles have been on the beach for some time or may have been refloated and migrated from their original landing points.

CALCULATED CURRENTS FROM GEOPOTENTIAL TOPOGRAPHY

Figure 3 shows the geopotential topography for the three periods August 1956, and February and August, 1957. The currents are presumed to flow along the isobars and the speed is inversely proportional to the distance between them. The general features of the circulation persisted from one period to the next. The mid-ocean movement was from the west and toward the North American coast at a rate of less than 2 miles per day (4 cm./sec.). The flow pattern divided, generally north of lat. 45°N., and part moved northeast and circulated around the Gulf of Alaska. The speed increased to the north along the Alaskan coast and peninsula, to about 4 to 6 miles per day (8 to 12 cm./sec.). The current continued westward along the southern shore of the Aleutian Islands. There was little evidence of re-circulation in the Alaska Gyral. The other portion turned southward to form the California Current and sub-Tropic circulation, resulting in a region of divergence.

The main differences between the three periods are: (1) The gyral was smaller in extent in August 1957 than in the two previous periods. Also, during this period, there is a relatively strong current extending eastward from the gyral (long. 147°W.) toward the coast, then a strong current relatively close to the coast. In the other periods only the strong current close to the coast was present, and was slightly closer to the coast in August 1956 than in the later periods. (2) Off the coast of Washington there was a more definite onshore movement in February than during the summer periods. (3) During the period February to August, 1957, there appeared to be an increasing tendency for southern water to intrude the area between Station PAPA and the Canadian coast.

INTERPRETATION OF DATA

Diagrams of geopotential topography prepared from the oceanographic data collected in the summer and winter surveys have been described. In the ideal case the flow would be along the isobars. However, in the real situation,

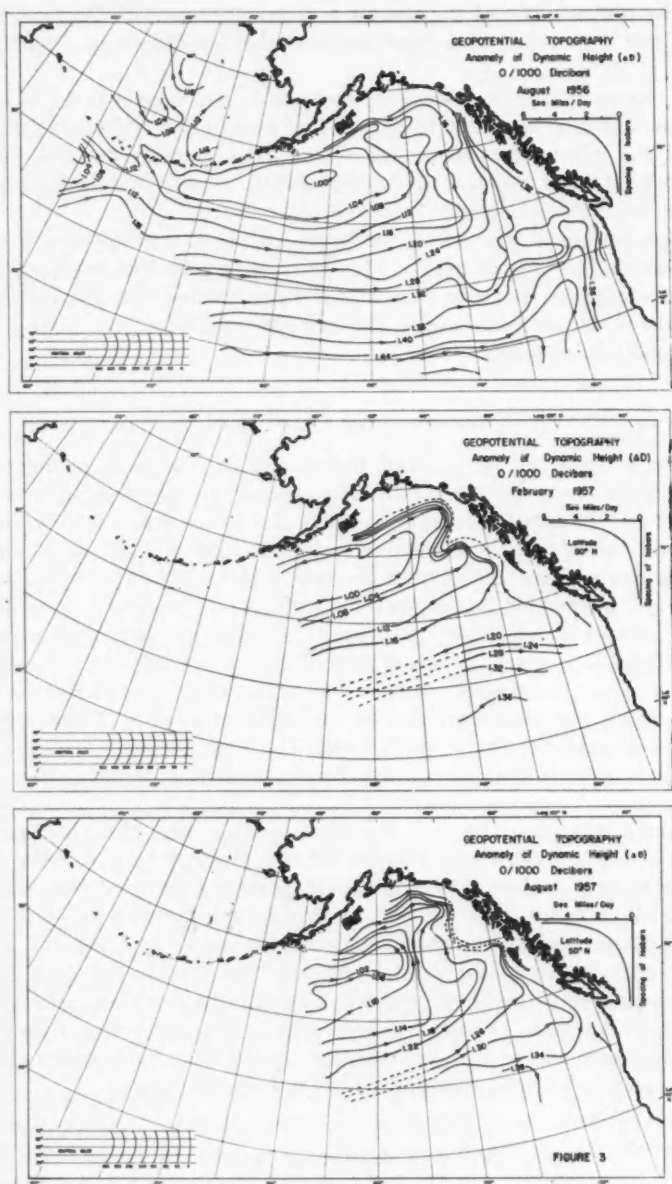


FIG. 3

where wind stress is added to the geostrophic forces there will be transport across the isobars. This is particularly true in the surface waters where the bottles floated.

The drift bottles were at sea for periods ranging from 4 months to a year. Hence, their behaviour cannot always be compared directly to the geopotential topography which represent the situation as it existed during the month required for the survey. However, these diagrams show that the major features of the circulation persisted throughout the year, and the line of flow apparently migrated persistently northward. The drift bottle data should confirm these major features.

The course of the drift bottles from the point of release was plotted along a reasonable path that would include the distribution of returns. In the mid-ocean the current patterns shown in the geopotential topography were borne in mind when plotting the drift path. Where there was no contradiction between the two sets of data, it is reasoned that they are mutually supporting.

The most probable time at sea was determined from the frequency distribution of the times of recovery on the beaches. The time unit was taken as 30 days. An example of these analyses showing the resulting frequency-distribution curve is given in Fig. 4. The curves for all releases generally have a similar form. The primary maxima are presumed to represent the direct drift and landing. There were secondary maxima that may be of some importance. However, the percentage of returns in these was too small to be significant, and they have been neglected. The releases with less than 1% recovery have also been neglected.

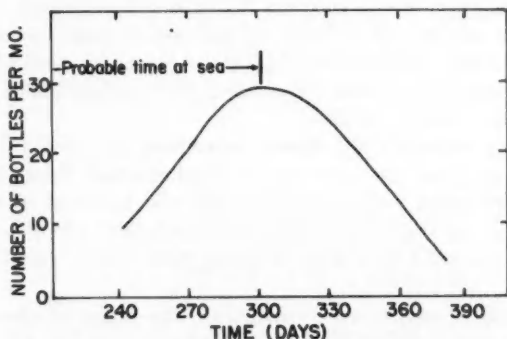


FIG. 4. Frequency-distribution curve of the returns from a release of 1,000 bottles at ocean weather station PAPA on August 25, 1956.

When the main body of the returns were from the Queen Charlotte Islands southward along the coast, the time at sea was not a function of the location of recovery. Frequency distributions in parts of the region were identical, and the same as for the whole. However, for the widely scattered returns which are

generally from the Alaskan coast the recovery area was arbitrarily subdivided (approximately 10° of longitude) and the frequency distribution for each region with respect to time was considered separately. These subdivisions have been reported separately in Table I.

RELEASES FROM OCEAN WEATHER STATION PAPA

The principal characteristics in surface flow were reflected in the returns from the releases made at Ocean Weather Station PAPA (Fig. 5-16). In every case the bottles arrived on the North American coast north of lat. 42°N . The first two releases (Fig. 5 and 6) approached the coast more or less latitudinally. Particularly noteworthy is the fact that the returns from the first release suggest a surface movement eastward with a southeasterly component. This movement is suggested in the calculated current system, if flow across the isobars is assumed. The second release had principally a northerly component.

After September 1956 there was a distinct northward shift of the returns (Fig. 7 and 8), suggesting a change in the surface circulation. However, the returns from the fifth release in January (Fig. 9) show that this distinct northward shift did not persist, since four returns from this release were found on the Washington coast. The returns from the releases during the period March-July (Fig. 10-13) indicate re-establishment of the northward movement; however it is not as pronounced as for the releases made in the previous winter. The returns from the latest releases (Fig. 14-16) show a definite northward shift, again suggesting a change in the circulation. This surface movement is reflected in the dynamic topography for this period and suggests that it is still persisting.

The returns indicate that there are definite surface movements into the coastal seaways during certain periods. This is especially marked in the returns from the second and sixth release (Fig. 6 and 10) in which there was a predominant movement into Dixon Entrance.

Other releases (Fig. 5, 6, 12) show a movement into Queen Charlotte Sound. It is difficult to determine the exact periods during which these movements were distinct; however Barber (1957) suggests that the intrusion of coastal seaways takes place during persistent south or southeast winds which occur principally during the winter months. It is suggested that these bottles moved in during this period.

Figures 5 and 17 show two returns from the Strait of Georgia. Evidently there was a surface movement through Juan de Fuca Strait. The Halibut Commission drift bottle programs (Thompson and Van Cleve, 1936) gave no such results, although they did show returns from the other coastal seaways.

RELEASES DURING NORTH PACIFIC OCEANOGRAPHIC SURVEYS

Figure 17 shows four releases made in August 1956. The most northerly one evidently circulated around the Alaska Gyral. The one on lat. 49°N . moved latitudinally toward the coast similar to the release made at Station PAPA during

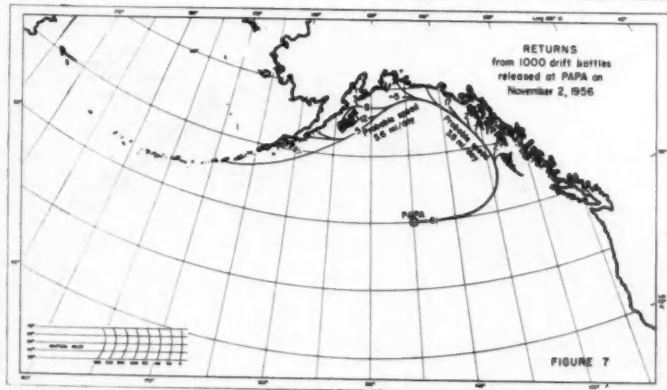
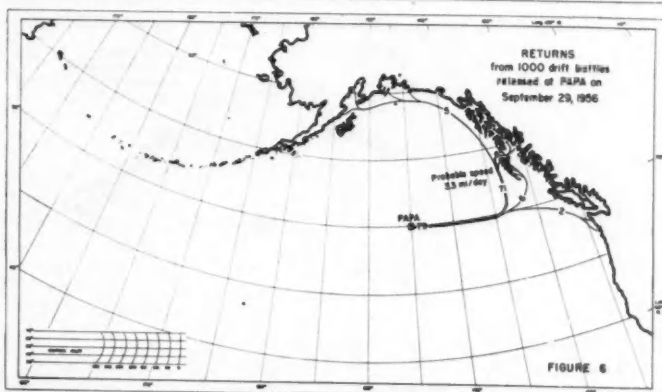
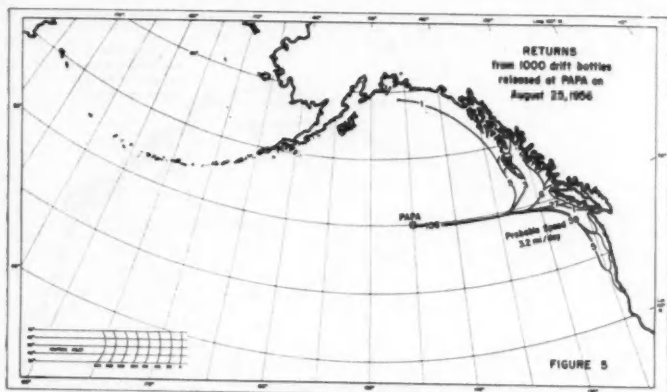


FIG. 5, 6, 7.

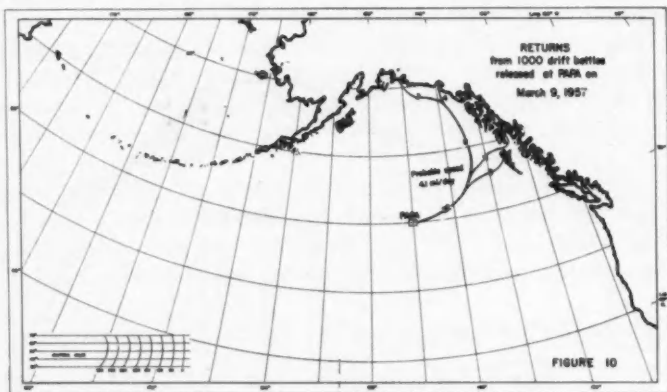
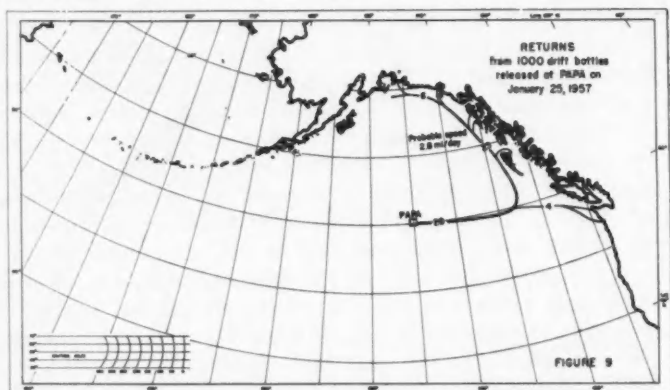
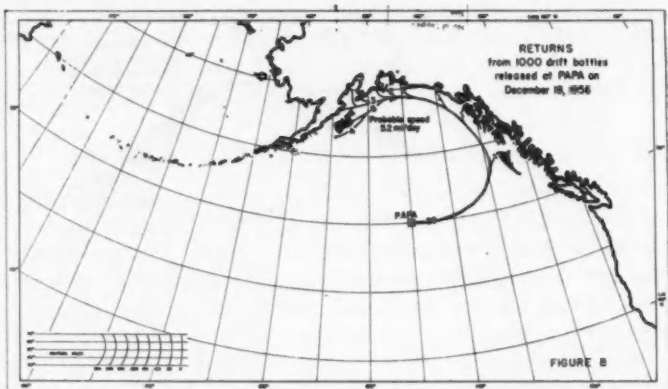


FIG. 8, 9, 10.

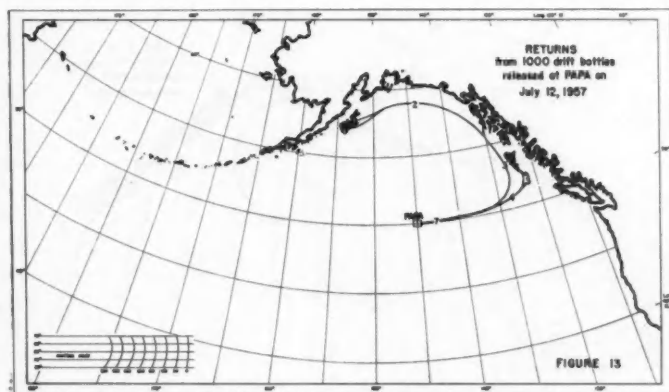
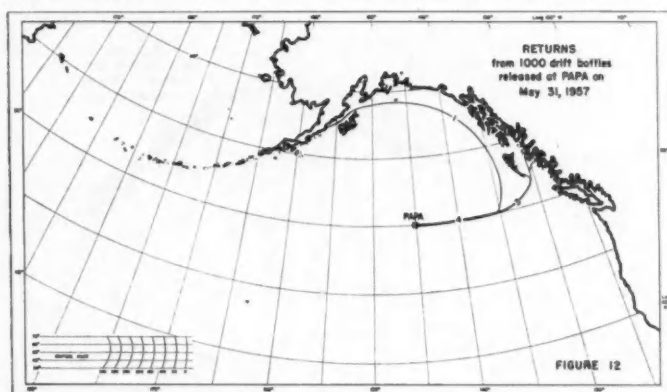
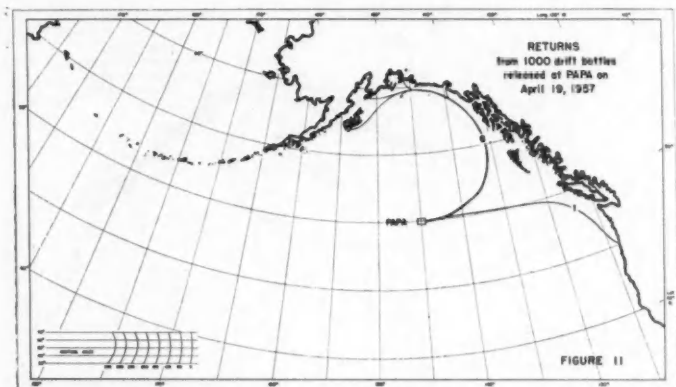


FIG. 11, 12, 13.

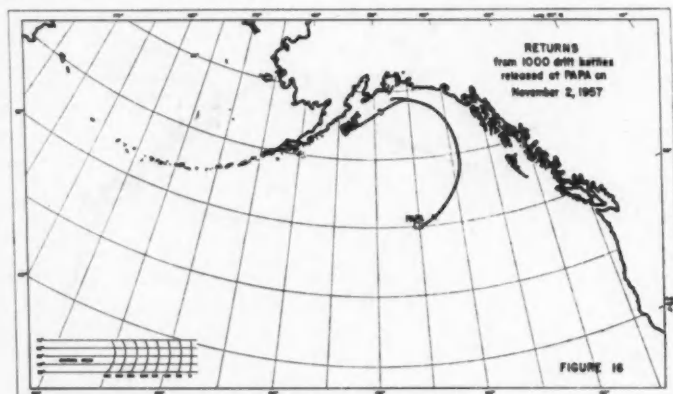
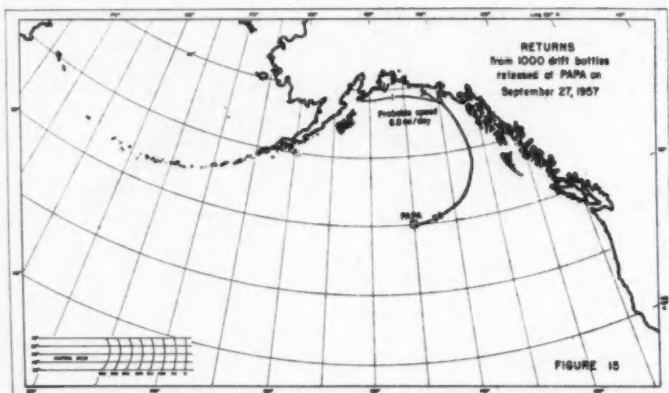
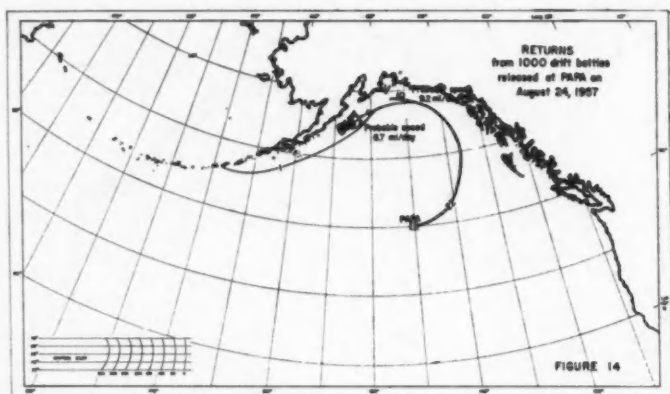


FIG. 14, 15, 16.

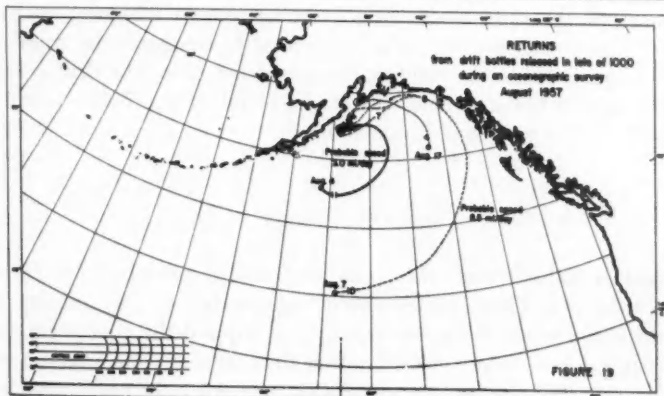
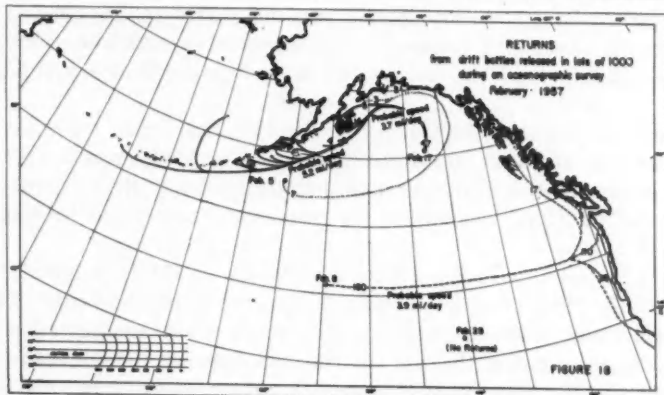
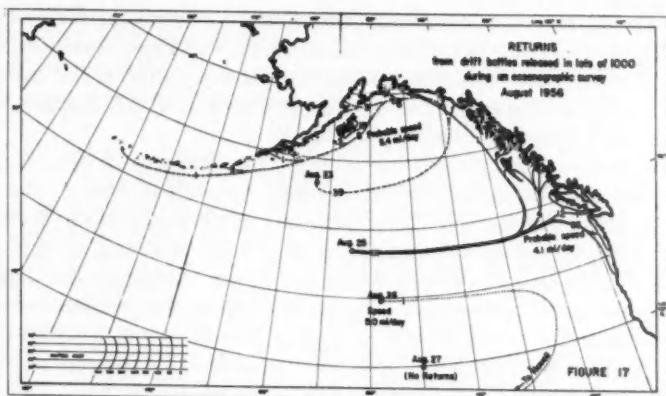


FIG. 17, 18, 19.

this same period. There has been one return from the Hawaiian Islands from the August 26 release. No returns have come from the most southerly release. Evidently the latter two releases were on the southern side of the divergence, and were carried southward in the sub-Tropic circulation. This implies that the divergence was between 45° and 48° N. latitude.

Figure 18 shows four releases made during the February 1957 survey. Again the two northernmost releases circulated around the Gulf of Alaska. The release on lat. 46° N. drifted latitudinally, principally to a small section of the Washington coast. The greatest percentage of these returns came within a 2-week period. There were no returns from the southernmost release. Evidently the divergence had moved southward between lat. 42° and 46° N. since the previous summer.

The southern shift of the divergence implies that there was a northward shift of current paths in the region of the Canadian coast. This is confirmed by the geopotential topography for the periods February and August 1957. The returns from a release (Fig. 19) on lat. 46° N. (August 7, 1957) confirms this, and also shows that the northward tendency was intensified far offshore. This is also consistent with data from the releases at Ocean Weather Station PAPA for this period.

The releases made in the Gulf of Alaska (Fig. 19) again show circulation around the Gyral. However, in this period none of the bottles reached the southwestern Alaskan coast as in the previous periods. Evidently the relatively strong current around the Gyral as shown by the geopotential topography for this period is confirmed.

There have been two returns from the vicinity of 175° E. longitude on the Aleutian Islands (Fig. 17 and 18) and one from the Pribiloff Islands (Fig. 18). These returns substantiate the westward flow south of the Aleutian Islands, and indicate surface dissipation through the channels between the Aleutian Islands.

Allowing for the anticipated transport of surface waters across the isobars, the consensus of the drift bottle data is in agreement with the geopotential topography. However it does emphasize the need to recognize the trans-isobaric drift which is generally to the right of the calculated flow. The drift bottle data do show the re-circulation around the Alaska Gyral (Fig. 17-19) which is not clearly evident in the geopotential topography.

SPEED OF DRIFT

The most probable speeds vary between 3 and 9 miles per day (6 and 18 cm./sec.) (Table I). These are generally comparable to the average speeds calculated from the geopotential topography and support the conclusion that the bottles are carried in a surface current rather than wind driven. It is noteworthy that since August 1957 the surface circulation was not only northward but the speed of the current was substantially faster than in the previous periods, of the order of 7 to 8.5 miles per day as compared to 3 to 5 miles per day. This suggests

that more water is flowing into the Gulf of Alaska, accompanied by a surface acceleration in the Alaskan Stream² to carry this water out of the gulf.

The one return from the Hawaiian Islands suggests a drift of about 5 miles per day in the sub-Tropic circulation.

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² Bennett (1958) has defined the Alaskan Stream as the strong current flowing south-westward along the southern side of the Alaskan Peninsula from Kodiak to Unimak Pass.



The Rivers Inlet Sockeye Salmon¹

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ABSTRACT

The Rivers Inlet sockeye catch has averaged about 1 million fish per year, over 45 years. These are from smolts produced in a cold, deep lake, only 30 square miles in extent, and most of it heavily silted by glacial tributaries. The water has only a moderate lime content and its reaction is neutral or very slightly acid. The lake's plankton crops are small, though blooms of bluegreen algae occur in autumn in the clear uppermost basins, following on the death of large numbers of spawning sockeye. Smolts are unusually small in size, averaging about 2 grams when sampled in 1914-16 and again in 1954; almost all are age 1. The commercial gill-net fishery harvests most efficiently the salmon of intermediate sizes: the medium and large age 4 fish, and the medium and small age 5 fish. Hence escapement tends to consist of extremes of size, the larger age 5's, smaller age 4's, and almost all the age 3's. Sockeye spawning takes place in many inlet streams, along parts of the lake shore, and in the outlet river. The spawners in the various tributaries differ considerably in respect to the age structure of their runs, and to some extent in size at a given age, though the selective fishery may account for some part of these differences. Conditions for spawning and incubation in the region are still practically in their natural state.

The most important management problem is to determine whether increasing the fry output into the lake would increase or decrease production of adult sockeye: the smolts are now so small that any larger numbers *might* possibly reduce their size below some critical level. Next in importance is to determine whether or not the present numbers of spawners are necessary to fertilize the lake for the growth of the young, and if so, whether a less valuable fertilizer might be substituted.

INTRODUCTION

DURING 1951 TO 1954 an investigation was conducted at Rivers Inlet, British Columbia, primarily for the purpose of determining what differences there are, in size and age, between the catch and the escapement of the sockeye salmon. Regular sampling of the catch had been done for many years, and has been reported in a series of papers published in the Annual Reports of the British Columbia Department of Fisheries (the latest is by Foskett and Jenkinson, 1957). However, because of the well-known selectivity of gill nets, it was desirable to ascertain how the fish escaping them differed in age, size and sex, from those which are caught.

In addition, information has been gathered on other aspects of the Rivers Inlet sockeye stock. Apart from the sampling just mentioned, the only published work on the biology of this stock is by Gilbert (1915, 1916, 1918), who described the seaward migrations and measured sockeye smolts taken in 1914-16.

Rivers Inlet's sockeye production is almost the best in British Columbia, in relation to the size of the watershed which maintains it. Catches have recently

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been summarized and graphed by Godfrey (1958). Since 1912 the catch has averaged about 1,000,000 sockeye per year, without any sustained trends upward or downward. These fish are from smolts produced in Owikeno Lake, whose area is only about 30 square miles. Being in a remote region, the lake has not yet been affected by agricultural or industrial development, or even by logging.

However, the large sustained yield of the Rivers Inlet stock should not lead to complacency. Apart from the likelihood that truly primitive conditions will not be maintained there much longer, there are the examples of other sockeye nurseries which produced at a high level for several decades, but later declined gradually or disastrously—sometimes in the absence of obvious physical reasons. Accordingly, it is desirable to learn as much as possible now about how Owikeno's excellent sockeye crop is produced, in order to guard against damage to it, perhaps even to improve it. The information presented here can serve as an introduction to this study.

PHYSICAL DESCRIPTION

PHYSIOGRAPHIC CONDITIONS

The Rivers Inlet watershed lies in a glaciated area with abundant rainfall, steep terrain and fairly heavy forest cover. The streams generally have steep gradients with falls relatively common. The soils are characteristically gravels with a thin layer of organic debris on the surface. In a few areas deltas are being built up in which considerable glacial silt is mixed with gravel.

Glaciers are still common in the mountains and several of the streams carry glacial silt. Two rivers, the Shumahalt and Machmell, come from large ice fields and are responsible for the fact that throughout the summer, autumn and part of the winter, light penetration into the greater part of the surface waters of Owikeno Lake is very restricted. At no time is the main body of the lake free of glacial silt.

CLIMATE

The climate of the Owikeno Lake area is one of strong winds and abundant rainfall. The closest rainfall gauging station lying in a similar position with respect to the coast is at Bella Bella, where the 23-year average through 1956 is 107 inches (272 cm.). There is evidence that the rainfall is greater at the upper end of the lake than at the outlet, though actual figures are lacking. Whether there is also a difference in temperatures is not known. The lake beyond First Narrows is reported to freeze over almost every winter, while below this point no complete ice cover has been observed by local inhabitants. This may, however, be due to the strong winds rather than difference in temperature.

OWIKENO LAKE

Owikeno Lake can be described as a fiord whose sill happened to be a little too high to maintain connection with salt water. The surface elevation is less than 50 feet (15 m.). The outlet stream flows about three miles to the Inlet, and most of it is affected by the tide.

The lake consists of a chain of four lakes or basins, here referred to as Basin 1, 2, 3 and 4, numbered from downstream up. The basins are separated by relatively shallow "narrows", and the whole is surrounded by high mountains with precipitous slopes (Fig. 1). There are no accurate surveys; the total water area

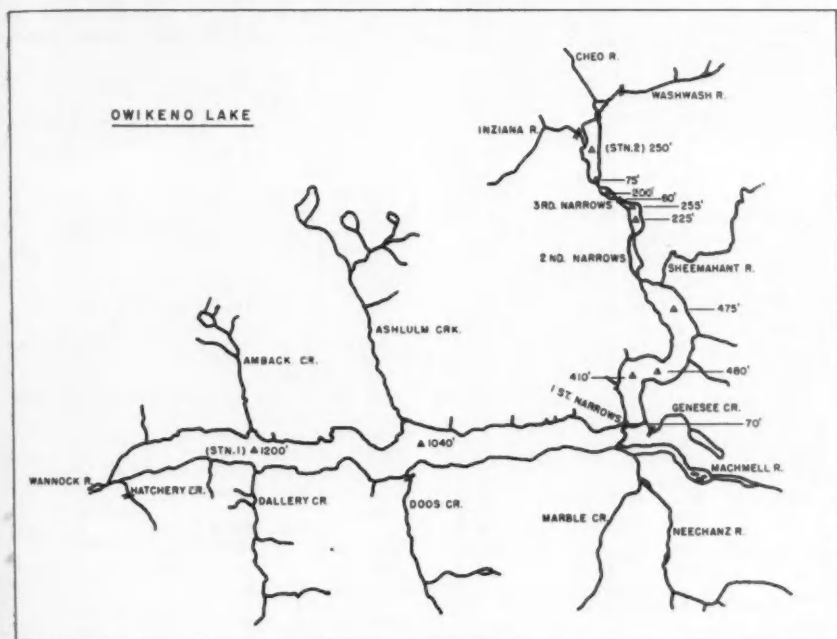


FIG. 1. Map of Owikeno Lake.

is about 30 square miles (78 sq. km.), as measured from existing maps, although the British Columbia Gazetteer (1953) estimates 34 square miles (88 sq. km.). The two lower basins are characterized by great depth and a heavy content of glacial silt. The two upper basins are free of visible glacial silt and are of more moderate depth. Maximum known depths are: Basin 1, 1,200 feet or 366 m.; Basin 2, 480 feet or 146 m.; Basin 3, 255 feet or 78 m.; Basin 4, 250 feet or 76 m. However, very little sounding has been done, particularly in the deep main basin.

The three narrows differ radically. First Narrows is a short narrows about 70 feet (21 m.) deep and 450 feet (137 m.) wide, between rock bluffs 300 to 400 feet high. Second Narrows is a broad shallow sluggish stream, 8-10 feet or 3 m. deep, characterized by extensive weed patches and occasional uprooted trees grounded in the mud. Third Narrows is a deep (200 ft., 61 m.) very narrow channel over a mile (1.6 km.) in length, with shallows of approximately 50 feet (15 m.) near each end. It is bordered by rock walls of close to 1,000 feet (300 m.) in height.

WATER TEMPERATURES

Scattered observations on surface temperatures are shown in Table I, taken in summer and early autumn. They mostly lie between 11° and 14°C. (52° and 57°F.).

TABLE I. Surface temperatures of Owikeno Lake, in degrees Centigrade. (Numbers in the left-hand column refer to bathythermograph casts made in 1952. In Figure 1, Stations 1 and 2 are located, and the unnumbered triangles correspond to the positions of many of the locations described below.)

No.	Date	Temperature °C.	Location
1	Aug. 31, 1952	11.5	Station No. 2, 4th Basin
2	Sept. 2, 1952	13.0	Station No. 1, 1st Basin
3	Sept. 11, 1952	11.5	Narrows north of Genessee
4, 6	Sept. 11, 1952	11.25	("Deep Narrows Station") halfway between Roaring Mack and Genessee Creeks
5	Sept. 11, 1952	12.0	Centre of First Narrows
7	Sept. 17, 1952	11.0	Lake north of Shumahalt flats
8	Sept. 19, 1952	11.25	Station No. 2, 4th Basin
9	Sept. 19, 1952	13.5	Centre of northern end of Third Narrows
10	Sept. 19, 1952	9.25	Halfway through Third Narrows
11	Sept. 19, 1952	10.0	Centre of southern end of Third Narrows
12	Sept. 20, 1952	11.0	One-third way from Shumahalt to Deep Narrows Station
13	Sept. 20, 1952	12.5	Two-thirds way from Shumahalt to Deep Narrows Station
14	Sept. 20, 1952	12.25	Deep Narrows Station
15	Sept. 26, 1952	12.25	Piles in Third Narrows
...	Sept. 26, 1952	11.5	Deep part of Third Narrows
16	Oct. 3, 1952	10.0	Centre of First Narrows
17	Oct. 8, 1952	12.0	Station 1
...	Oct. 15, 1953	8.8	Just off Inziana River
...	July 4, 1954	10.5	Station 2
...	July 5, 1954	9.3	Station 1
...	Oct. 14, 1954	6.25	Station 2
...	May 27, 1956	4.75	Station 1A

Bathythermograph casts were made at Station 1A on May 27, 1956, when the lake was still practically homothermal: the temperature varied from 37.3°F. at 150 feet depth (49 m.) to 38.0° at 20 feet (6.5 m.), rising to 40.5° at the surface. In September and early October of 1952 vertical distribution of temperature was examined at a number of points in the three upper Basins and at Station 1 in Basin 1 (Fig. 2). At this time there was a well-developed thermocline centered at about 100 feet (33 m.) in the upper basins, while in the main lake at Station 1 the thermocline was thicker, with not so sharp a gradient, and centered about 170 feet (56 m.).

CHEMICAL COMPOSITION OF THE LAKE WATER

Analyses of five samples of water from Owikeno Lake have been made (Table II). Two of these samples were of surface water from the uppermost basin of the lake (Station 2); two were of surface water in the main basin of the lake (one at Station 1 and one off Hatchery Point which is nearer the outlet than Station 1) and the fifth sample was from the deep water (1,000 feet) at Station 1.

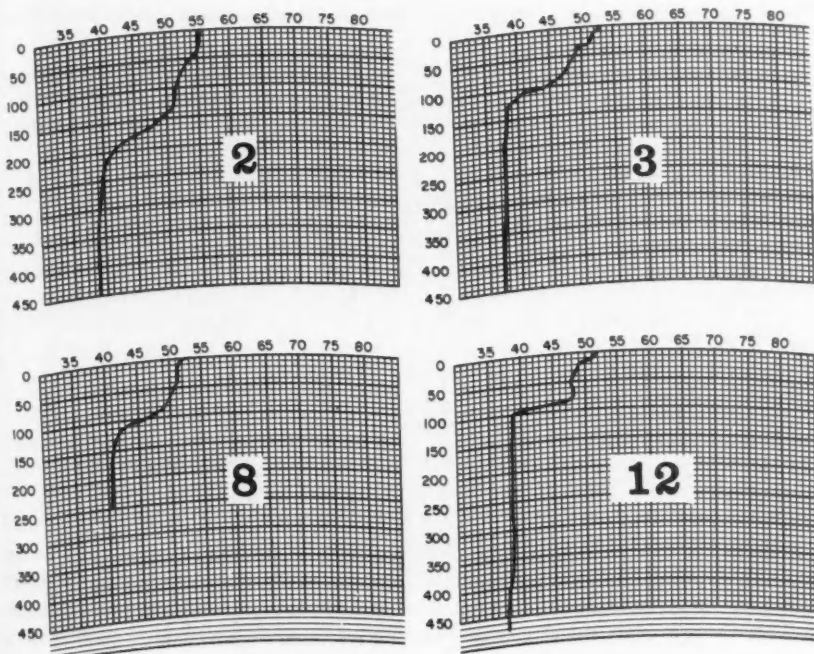


FIG. 2. Bathythermograph tracings taken from Owikeno Lake. Depth scale in feet; temperature in degrees Fahrenheit.

Tracing No. 2, September 2, 1952, Basin 1 at Station 1: between Quap and Dallery Creeks. Bottom at 1200 feet.

Tracing No. 3, September 11, 1952, Basin 2 in the bend north of Genesee Creek. Bottom at 480 feet.

Tracing No. 8, September 19, 1952. Basin 4 at Station 2. Bottom at 250 feet.

Tracing No. 12, September 20, 1952. Basin 2 in northern part. Bottom at 475 feet.

Surface samples at Station 1 show conditions when the glacial silt content in the water was very low (July sample) and when it was quite high (October sample). (In normal years silt in the lake would be fairly high in early July, but due to a very cold spring in 1954 the glaciers had not melted to any extent at that time.)

PLANKTON

Plankton samples in Owikeno Lake were taken with a Wisconsin type net using #20 silk bolting cloth. The samples were taken at Stations 1 and 2, and at other points. In general, plankton was not abundant.

Diatoms have tended to be the most abundant plant plankters, except at places and times when there were blooms of blue-green algae. Among the diatoms, *Tabellaria* and *Fragilaria* were the most prevalent forms.

TABLE II. Analyses of waters of Owikeno Lake from the surface and from a depth of 1,000 feet. Figures are in parts per million (except pH).

	Station 1 Surface Oct. 14, 1953	Station 1 Surface Early July, 1954	Station 2 Surface Oct. 15, 1953	Station 2 Surface Early July, 1954	Station 1 1000 feet Oct. 15, 1953
Reaction (pH)	6.9	7.0	6.3	6.8	7.0
Colour (Pt-Co standard)	7.5	12.5	19.0	7.5	7.5
Turbidity	16.5	2	2.0	2	2
Alkalinity					
Carbonates	nil	nil	nil	nil	nil
Bicarbonates (HCO ₃)	15.9	17.1	12.2	9.8	17.1
Total dissolved solids	35	19.0	22	25.0	30.0
Fixed solids	25	14.0	14	16.0	21.0
Volatile solids	10	5.0	8	9.0	9.0
Analysis of fixed solids					
Silica (SiO ₂)	5.6	2.0	2.6	2.0	2.0
Iron & aluminum oxides (Fe ₂ O ₃ + Al ₂ O ₃)	1.8	1.4	0.4	2.0	1.5
Calcium oxide (CaO)	3.7	4.0	3.3	3.0	6.0
Magnesium oxide (MgO)	1.4	0.7	0.6	0.6	0.7
Sulphur trioxide (SO ₃)	nil	1.4	nil	0.7	2.2
Chlorides (Cl)	1.5	3.4	0.5	2.0	7.5
Undetermined alkalies, etc. (by difference)	3.9	1.1	2.6	5.8	1.1

Blooms of Cyanophyceae were observed only in the late fall, and only when very heavy runs of sockeye had occurred a few weeks earlier. The blooms showed up as rows of green along the shores, and blue-green algae clogged the plankton nets when hauls were made in the open water. They occurred only in Basins 3 and 4. Their absence from the two lower basins could be a result of the heavy silt load, or because the greater volume of water there lowered the concentration of the fertilizer, or both. I have observed the same phenomenon under the same circumstances at Bear Lake in the Skeena River drainage, and conclude that such blooms are due to the heavy fertilization of the lake by the disintegrating sockeye carcasses.

Rotifers were dominant in the zooplankton samples, with *Polyarthra* the most abundant form. *Daphnia longispina* was the most numerous cladoceran in the samples, and *Cyclops* the most numerous copepod genus. Several kinds of the larger Protozoa were present in the samples and amongst these the stalked form, *Dinobryon*, was dominant.

LIFE HISTORY OF RIVERS INLET SOCKEYE

EGGS AND FRY

The sockeye eggs, in common with those of other Pacific salmon, are fertilized immediately after being expressed from the female and are then buried in the gravel. Though this usually takes place in a clear stream, in the Rivers Inlet area it may take place in either clear water, or water containing glacial silt, and the eggs may be deposited in the gravel of a stream or in gravel in the lake. Where spawning occurs in the lake there is either a definite current, as in the Shumahl Narrows, or the redds lie off the mouths of small valleys where there is probably seepage into the lake through the gravel from the stream above.

Once the fry become free swimming they must start looking for food. Fry hatched in the inlet streams will reach the lake by moving downstream. There is also a considerable adult sockeye run which spawns in the upper part of the Wannock River, the outlet stream of Owikeno Lake. These fry have two alternatives, either they can go downstream to the sea or upstream to the lake. With regard to the former, there are very few fish of fry-run type in samples of the Rivers Inlet sockeye catch. Gilbert (1915) recorded the capture of sockeye fry during seining operations for seaward migrants, and presumed that these were migrating seaward. From information received from Fisheries Overseer Stone's brother, the seining of fry and yearlings for Dr. Gilbert's use was carried out not only in the outlet of the lake, but off the mouths of some of the spawning streams. In any event, fry caught in the Wannock River could have been migrating upstream to the lake, as they are known to do in the outlet streams of some other lakes. Thus, there is no evidence that the fry taken were actually migrating to the sea.

FINGERLINGS AND SMOLTS

Dr. Gilbert (1915, etc.) has shown that the Rivers Inlet sockeye grow very slowly in the lake during their first year, up to the time the first scale annulus is formed, but that they put on considerable growth in the next season before migrating from the lake. This is in contrast to the usual picture in other areas, where there is seldom much growth shown on scales of migrants at the time they leave the lake, beyond the winter check. Plankton samples show that food is not abundant in the lake during the summer, but it may be more abundant in the fall.

In spite of this "additional" spring growth, the size at which Owikeno sockeye smolts go to sea is unusually small. The samples measured by Gilbert were taken throughout almost the whole season of migration in 1914, 1915 and 1916—many hundreds of fish in all. They indicate a gradual *decrease* in size as the season progresses, amounting to about 10 mm. in 1916 (see figure 31 of Clutter and Whitesel, 1956). Average fork lengths are given by Gilbert (1918, p. 66) as 58.6 mm. in 1914, 59.7 mm. in 1915 and 59.6 mm. in 1916, though the seasonal variation suggests that any of these might be out by 1 or 2 mm. either way. For recent years, samples containing about 2,000 smolts were taken May 28–29, 1956, by seining in the lake at Hatchery Point, not far from the outlet. They averaged 61 mm. in fork length and 2.0 g. in weight, showing that smolt sizes to-day are much the same as in Gilbert's day—if anything, not quite so small.

Even to-day, however, these are really tiny smolts—among the smallest known. Some comparative data for British Columbia are given in Table III. Of the runs shown, only the Shuswap Lake smolts of the dominant line are of comparable size—being of exactly the same average weight as Owikeno in 1952, and half a gram larger in 1948. Johnson (1956) showed that in 1955 a portion of the Babine system contained dense populations of slow-growing sockeye: for example, the fish sampled in Nilkitkwá Lake averaged 1.13 g. in mid-October, and would probably scarcely have reached 2 g. by migration time the following spring.

TABLE III. Comparison of size of Owikeno sockeye smolts with yearling smolts of other British Columbia runs. (After various authors.)

River system	Run	No. of years	Mean of av. yearling weights	Range of av. weights	Reference
			g.	g.	
Rivers Inlet	Owikeno	1	2.0	...	This paper
Skeena	Babine ^a	5	4.9	3.8-5.6	Data of F. C. Withler
Skeena	Bear Lake	2	8.7	7.8-9.6	Data of K. V. Aro
Skeena	Lakelse	5	5.6	4.6-6.3	Data of M. P. Shepard
Fraser	Cultus ^b	9	6.1	3.1-8.1	Foerster, 1944, table 2
Fraser	Chilko	4	4.1	3.3-5.1	Clutter and Whitesel, 1956, table 5
Fraser	Francois	1	12.0	...	Do.
Fraser	Harrison	1	9.2	...	Do.
Fraser	Horsefly	1	19.5	...	Do.
Fraser	Lillooet	1	4.5	...	Do.
Fraser	Shuswap ^c	2	2.3	2.0-2.6	Do.
Fraser	Stuart	1	8.4	...	Do.

^aThe Babine River smolts are a mixture of small smolts from most of the North Arm and from Nilkitkwa Lake, and larger smolts from the rest of Babine Lake (Johnson, 1956).

^bThe years quoted are 1927-35, representing "natural" conditions prior to predator control on this lake. Later both larger and smaller smolts were observed (av. 8.8 g. in 1936, 2.7 g. in 1941).

^cThe years represented (1948 and 1952) both belong to the very numerous dominant sockeye line at Shuswap. Lengths given for one other year, by Clutter and Whitesel, indicate larger smolts in the poor lines.

Apart from these examples, however, the usual average size for British Columbia sockeye smolts is 4 to 8 g., and much larger ones are known.

From the dates of Dr. Gilbert's samples, the migration of yearling sockeye from Owikeno Lake to the sea occurs during May and the first part of June. Once these fish reach the sea their growth is not as rapid as is customary in populations of sockeye from the Fraser, Nass and Skeena Rivers, but it is similar to that of the Nimpkish, Smith Inlet, Bella Coola and Kimsquit River populations (Gilbert, 1915).

OCEAN LIFE

As with other British Columbia sockeye populations, there is little definite information concerning the whereabouts of Rivers Inlet sockeye in the ocean at the time they make their sea growth. During coho tagging operations off Quatsino Sound, Vancouver Island, in 1949, a number of sockeye were caught on the trolls and tagged. Two of these were recaptured in Rivers Inlet. Thus, it is known that some Rivers Inlet fish feed at least as far away as this area, but they probably go much farther.

CATCH

On returning to Rivers Inlet on their spawning migration, the sockeye presumably first enter the fishery in Queen Charlotte Sound. From the area off the mouth of the Inlet to the fishery boundary a few miles from its head, the fish pass through a maze of gill nets. The sizes and ages represented in samples of the commercial catches in the Rivers Inlet area have been published for many years (Foskett and Jenkinson, 1957, and earlier papers in this series). These samples

represent the catch moderately well, but are not weighted exactly as the daily landings. The length distributions of samples of sockeye caught in 1952 are shown in Figure 3.

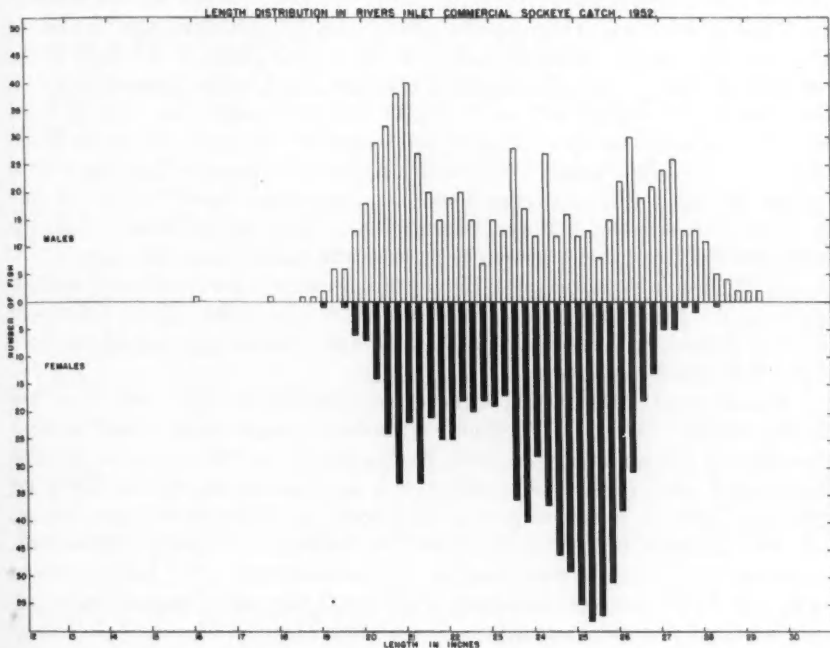


FIG. 3. Length distribution of the sample of the Rivers Inlet sockeye catch in 1952.

ESCAPEMENT

Sockeye spawn in the Owikeno Lake outlet, the Wannock* (Whonnock) River,³ in numerous tributary streams, and at various places in the lake itself. Estimates of spawning stocks are made annually by the Fisheries Overseer or Guardian, but floods, silt and limited time make it a difficult task. The Wannock is one of the important spawning rivers, and has several times been estimated to have over 50,000 sockeye. Main spawning tributaries of Basin 1 of the lake are the Quap (Amback) River and Asklum (Ashlulm) Creek on the north side, and Dallery* (Dallec) Creek on the south; also on the south near the outlet is the small Hatchery or Me-dow-se Creek. At the head of Basin 1 is the large Machmell* (Markwell) River, whose silt-laden waters make estimation of

³Names used for Owikeno Lake tributaries are not yet stabilized; even the name of the lake is often spelled Owekeno or Owekano. In the text we give first the name approved by the 1953 British Columbia Gazetteer, when one was located in it (such are marked by an asterisk); this is followed by any important variant which has the sanction of present-day local usage. The older literature has still other forms, of course.

salmon spawners by inspection almost impossible. Near its mouth enters the Nuchanz (Neechanz or Nookins) River, a large stream, also rather muddy in summer. Immediately above the First Narrows the Genesee* River, draining Walkus Lake, usually has a run of the order of 10,000. At the Second Narrows the glacial Shumahalt (Sheemahant) River usually contains large bodies of spawners, as does the adjacent shallows or Shumahalt Flats. At the head of the fourth basin there is the clear Inziana* (Indian) River, whose spawning area is short but densely stocked with up to 100,000 sockeye or more; the Tzeo* (Cheo) River flowing from the north is larger and somewhat muddier, with up to 20,000 sockeye; and the Waukwash (Washwash) River is estimated to have from 5,000 to over 100,000 in different years. There are also smaller creeks which are used by a few spawners; for example, Roaring Mack Creek enters Basin 2 from the west, while Whiskey and Sunday Creeks flow into Basin 3 from the east.

In addition to the spawners in the rivers and creeks, large numbers of sockeye spawn in the lake itself: on the "flats" just above the outlet, off the mouths of creeks and rivers, in the Second and Third Narrows, and along much of the shore of the Third and Fourth Basins.

Measurements of spawning sockeye are available for 1952, and for a few streams in 1955 (Tables IV, V). Figure 4 shows the length distributions for dead specimens at certain streams in 1952. Even allowing for the smallness of some samples and other vagaries of sampling, it is nevertheless evident that there are differences between runs in respect to the proportions of the various ages present, and even in respect to the size distribution of the fish of a given age. Three-year-old sockeye, which can be considered as approximately those of 17 inches (mature fork length) and less, were numerous at Dallery, Quap and Genesee Creeks, but were relatively uncommon elsewhere. Considering 24 inches (mature fork length) to be the approximate division between 4₂ and 5₂ males, fish of the 5₂ group were dominant at the Inziana and Nuchanz Rivers, were in a substantial majority at Waukwash and possibly Asklum, were about on a par with 4-year-olds at Dallery River, Quap Creek and Genesee Creek, were quite scarce at Shumahalt River and Whiskey Creek, and were not found at all in the Wannock River. The size of the males at a given age also differs between streams: for example, where they are scarce, 3-year-olds tend to be larger than average; the 5-year-olds of the Inziana, Nuchanz and Waukwash Rivers exceed those of Dallery and Quap; Wannock River 4's are larger than average; and so on.

In a given stream females tend to deviate from average in the same direction as do the males there, both in respect to age frequency and in size at a given age; but their overall variability is less, and of course there are no 3-year-old females.

For the Dallery River, age compositions of both males and females were in general similar in 1952 and 1955, but the average size of 4₂'s and 5₂'s of both sexes was somewhat smaller in 1955.

Except for those involving the 3-year-old males, none of these differences between streams need be wholly of biological (racial) origin; the fishery very probably plays a part. The earlier runs, like those to the Waukwash and Inziana Rivers, may be exposed to a heavier fishery and hence more severe selection for

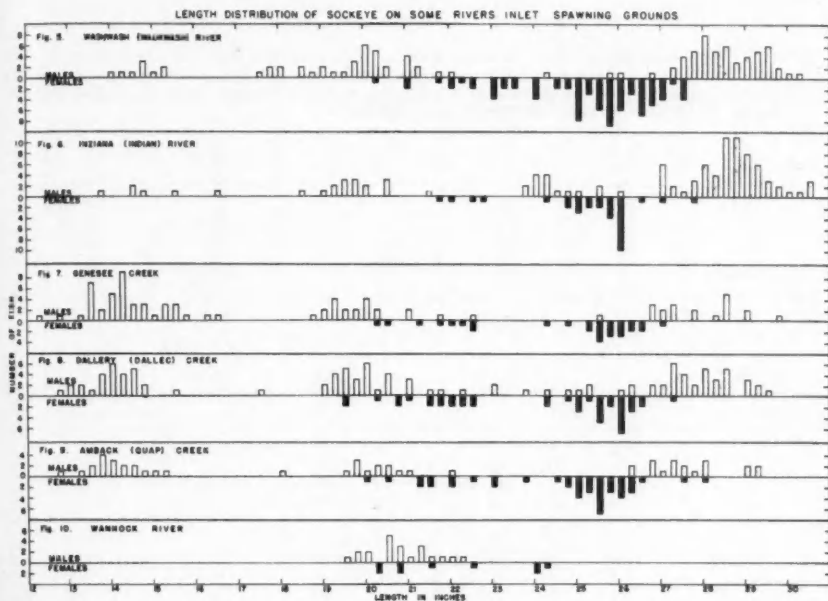


FIG. 4. Length distributions of dead spawners taken at the various spawning streams in 1952.

size, which might partly account for the *relative* abundance and large size of the 5_2 males there. It is apparent, however, that biological differences between the stocks returning to spawn in different streams do exist. There may even be some suggestion of associations between the size of the fish and the position or nature of the spawning stream. More years' observations will be needed to determine the exact degree of distinctness between the different spawning stocks, and the degree of year-to-year consistency in their size and ages.

COMPARISON OF CATCH AND ESCAPEMENT

Comparison of catch and escapement is made difficult by two circumstances: 1. scales of breeding fish are so resorbed that their complete growth history is rarely indicated; and 2. the preorbital portion of the head lengthens with maturity, changing the overall length of the fish. The latter change is much greater among males than among females; it also varies between individuals and to some extent between different sockeye races. The average increase in fork length is of the order of 5% for males and 1% for females. Compensating it to some extent, when working with old or dead fish, is a tendency for the skin and tips of the rays of the tail to wear off, and for some skin to wear off the nose, though of course obviously frayed or damaged specimens are not measured. The detailed measurements that would be necessary to establish adjustment factors between green and spent fish are not available, but for preliminary orientation it is assumed

TABLE IV. Fork lengths, in inches, of dead male sockeye collected from the Owikeno spawning grounds. Samples were taken in 1952 except as noted. The last line gives an estimate of the 1952 abundance of spawners (both sexes) according to the following scale: K, 10,000-20,000; L, 20,000-50,000; M, 50,000-100,000; N, over 100,000.

Mid-class length	Wannock	Quap	Dallery, 1952	Dallery, 1955	Askum	Nuchanz	Genesee	Shumahalt Flats	Shumahalt River, 1955	Whiskey	Iniziana	Waukwash
<i>inches</i>												
12	1
12.25	0
12.5	1
12.75	...	1	1
13	...	0	2	1	0
	...	1	2	0	1
	...	2	1	1	...	1	7
	...	4	4	0	...	0	2	1	...
14	...	3	6	2	0	1	5	0	1
	...	2	4	0	1	...	9	0	1
	...	2	5	3	0	...	3	2	1
	...	1	2	0	0	...	3	1	1	3
15	...	1	0	4	1	...	1	0	1
	...	1	0	3	0	2
	1	3	1	...
	1	0	...
16	0	0	...
	1	0	...
	1	1	1	...
	0
17	3
	0
	1	1	1	...	1
	0	0	3	0	...	2
18	...	1	0	10	1	0	...	2
	...	0	0	1	0	0	...	0
	...	0	0	5	1	1	1	1	2
	...	0	0	0	1	0	2	0	0	1
19	...	0	2	7	...	1	2	1	3	1	1	2
	...	0	4	1	1	...	4	1	3	3	2	1
	...	1	1	5	4	1	2	1	0	1	3	1
	...	2	3	3	1	1	2	0	1	1	3	3
20	...	2	1	6	5	0	4	0	1	5	2	6
	...	0	2	1	0	0	2	1	0	4	0	5
	...	5	2	4	1	0	0	1	0	1	3	2
	...	3	1	0	0	1	0	1	0	1	0	0

Mid-class length	Wannock	Quap	Dallery, 1952	Dallery, 1955	Askum	Nuchanz	Genesee	Shumahalt Flats	Shumahalt River, 1955	Whiskey	Inziana	Waukwash
inches												
21	1 3 1 1	1 0 0 0	3 0 1 1	0 0 4 0	0 0 0 0	...	2 0 0 1	2 0 0 1	0 1 ...	1 0 0 0	0 0 1 ...	4 2 0 1
22	1 1 ...	1 ...	0 1 ...	2 0 1	0 0 1	...	0 0 1	0 0 0 1	...	1 ...
23	2 0 0 1
24	0 1 0 1	0 0 0 0	...	1 0 0 0	0 0 1 0	...	3 3 1 1	...
25	1 2 0 0	1 0 0 0	...	0 1 0 0	...	1 ...	0 0 0 0	...	1 0 2 0	0 0 0 1
26	1 2 0 3	5 0 4 1	0 0 1 0	0 0 2 0	0 0 0 3	...	0 0 0 0	...	1 0 0 0	1 0 0 1
27	...	1 3 2 1	2 6 4 2	2 1 3 0	0 0 0 2	0 1 0 0	2 3 0 2	...	0 1 1 0	...	6 2 1 3	0 2 4 5
28	...	3 0 0 0	5 2 6 0	1 0 0 1	2 1 0 1	1 0 4 2	0 1 5 0	...	1	6 4 11 11	8 5 6 3
29	...	2 2 ...	3 2 1	...	3 ...	2 0 1 0	2 0 0 1	8 6 3 2	4 5 6 2
30	1 1	1 1 3	1 1 ...
Total Abundance	21 M	50 M	106 N	79	19 L	20 L	83 K	11 M	25	24	104 L-M	101 N

TABLE V. Fork lengths in inches of dead female sockeye collected from the spawning grounds. Samples were taken in 1952 except as noted.

Mid-class length	Wannock	Quap	Dallery, 1952	Dallery, 1955	Askum	Nuchanz	Genesee	Shumahalt Flats	Shumahalt River, 1955	Whiskey	Inziana	Waukwash
<i>inches</i>												
19	3
	2	0
	0	0
20	...	1	0	5	1
	2	0	1	0	1	...	1	1
	0	1	0	1	1	...	0	0
	2	0	2	1	0	...	0	0
21	0	0	1	1	0	...	1	0	0	2
	0	2	0	0	...	1	1	...	2	1	0	0
	1	2	2	3	...	0	0	...	0	1	0	0
	0	0	2	0	1	1	1	...	0	0	1	1
22	0	2	2	2	0	0	1	1	...	2	1	2
	0	2	2	0	1	0	1	0	0	1
	1	1	2	0	1	0	2	0	1	2
	...	0	...	0	0	1	0	1	0
23	...	2	...	1	0	0	1	...	4
	...	0	...	1	1	0	2
	...	0	...	2	1	1	2
	...	1	...	0	1	0
24	2	0	...	6	1	1	4
	1	0	2	7	1	...	1	1	0
	...	1	0	0	0	2	0	0	2
	...	2	1	0	0	2	1	2	2
25	...	4	3	10	0	4	0	1	3	8
	...	3	1	0	2	1	2	1	2	3
	...	7	5	6	2	3	4	1	2	6
	...	3	2	0	4	1	3	0	4	9
26	...	4	7	1	1	6	3	2	10	6
	...	3	3	...	0	0	2	1	0	2
	...	1	2	...	2	4	2	1	7
	...	0	0	...	0	2	0	0	5
27	...	0	0	...	3	1	1	1	1	4
	...	0	1	0	1
	...	1	1	0	4
	...	0	1	...
28	...	1
Total	9	42	43	50	22	30	27	3	5	12	31	80

that the average *net* change in fork length among males is an increase of 4%, while for females it is less than 1% and not great enough to concern us. In Figure 7, below, the mid-point of each length-class of mature males is reduced by dividing by 1.04, making the scale of the frequency distribution more comparable to that of the green fish taken by the fishery.

A more serious difficulty is presented by the impossibility of weighting the Owikeno spawning-ground samples in terms of the abundance of each run involved; moreover, studies elsewhere show that larger sockeye tend to be more "recoverable" than smaller ones, so that the larger fish are probably over-represented. However, for preliminary orientation we have merely combined all the samples available in 1952 into a single frequency distribution for each sex (Fig. 5). Each sex is compared with the corresponding catches in Figure 6-8, Figure 7 being the "adjusted" graph for males.

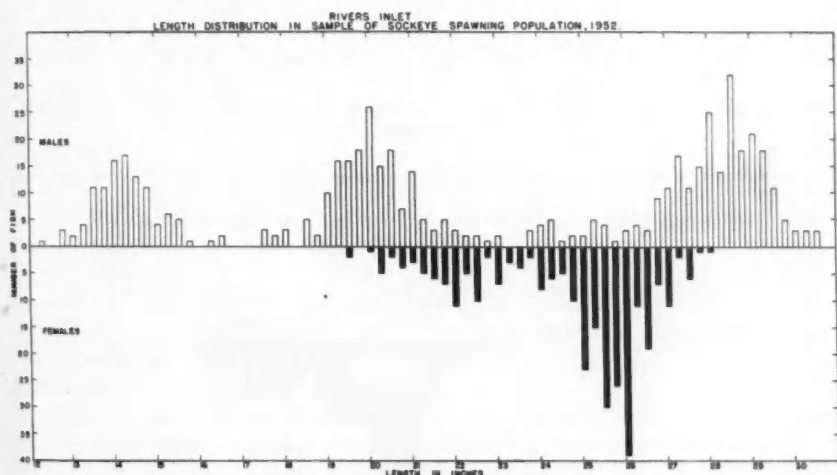


FIG. 5. Sizes of male and female escapement in 1952 (all samples combined).

Considering males first, the most obvious difference between catch and escapement is the almost complete absence of 3-year-olds in the catch. Among older males, age-groups 4_2 and 5_2 are the only ones present in significant numbers (the very few 5_3 fish fall into the length range of the 4_2 's). In the catch these two groups form a trimodal distribution, the modal lengths (allowing for sampling variability) being about 21 inches for 4_2 's, 26.5 inches for 5_2 's, and 23.75 inches in the region of overlap of the two groups. Among spawners, the most representative (adjusted) lengths is down to about 19.5 inches for 4_2 's, it is as great as 27.25 inches for 5_2 's, while the central range of lengths is a broad depression represented by very few fish (Fig. 7). There is a strong presumption, therefore, that the gill-net fishery selectively removes far more of the medium-sized fish

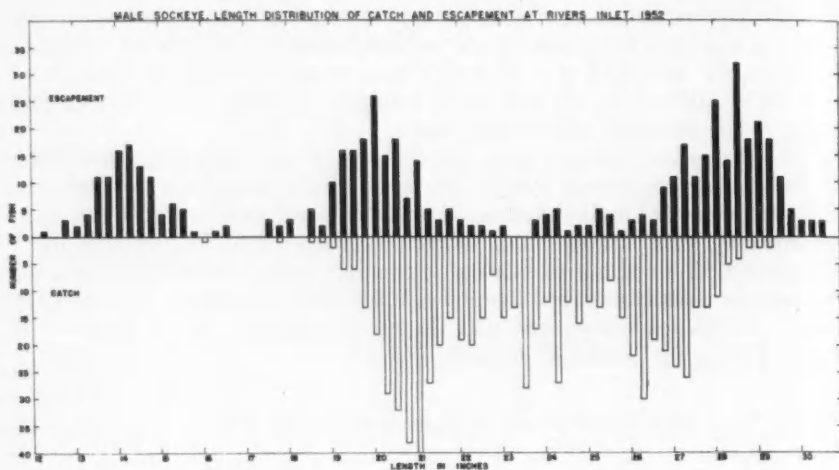


FIG. 6. Length distribution of catch and escapement of male sockeye in 1952 (fork lengths, as measured).

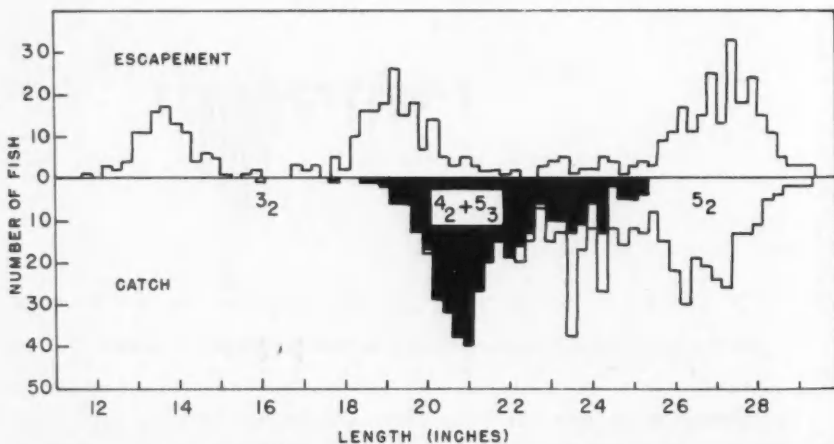


FIG. 7. Size distribution of catch and escapement of male sockeye in 1952 (fork lengths; escapement lengths are reduced by dividing 1.04). The age composition of the catch is indicated by the 4_2 (plus 5_3) fish being shown in black, while 3_2 and 5_2 fish are left clear.

than of the extremes of size: the smaller of the 4_2 's and the larger of the 5_2 's are relatively much less used.

A similar but not identical picture is indicated for females (Fig. 8). In the escapement there is a preponderance of large 5_2 females, and a scarcity of small 5_2 's and of the largest 4_2 's, just as in the males; but the smallest 4_2 females do not

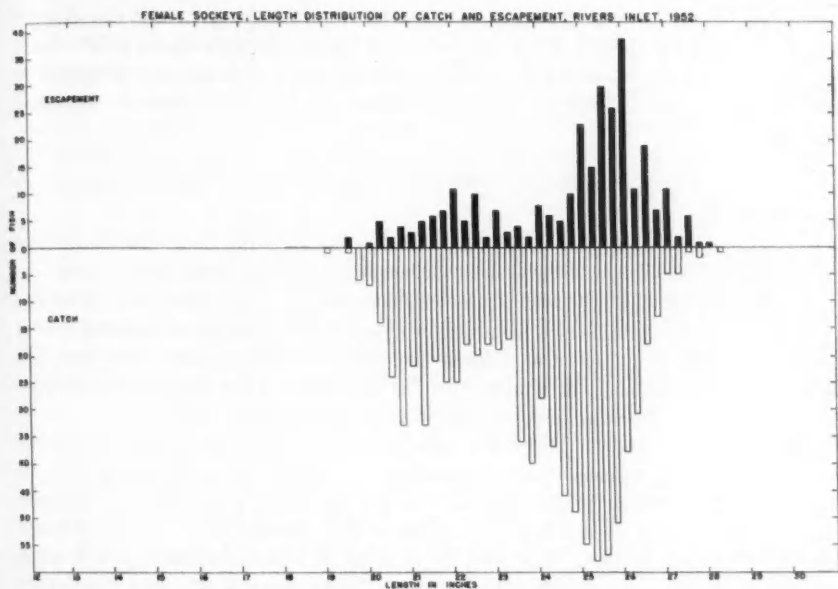


FIG. 8. Size distribution of catch and escapement of female sockeye in 1952 (fork lengths, as measured).

appear in the escapement in the same relatively large numbers as small 4_2 males. Either small female 4_2 's are really scarce relative to males of the same size, or else the conditions of distribution and sampling make it difficult to obtain the smallest females after spawning.

One net result of the selectivity of the gear in 1952 was to remove more females than males from the stock. The 3_2 males were practically untouched by the nets, but even among older fish the proportion of males in the catch samples was 44% (692 out of 1,567), whereas in the spawning ground samples it was 59% males (431 out of 730).

There have been complaints in some years of losses of sockeye, chiefly the very large males, as a result of "partial gilling" in the gill nets. The head enters the net until the opercula are held tight and the fish suffocates, but it is not gilled. The sockeye then remains there until the net is lifted from the water; during lifting the weight of the fish, aided by the tossing of the boat causes the salmon to fall from the net. The fish then sinks to the bottom and is lost to both the fishery and the spawning run. It is difficult to assess the true amount of loss suffered in this way, and not all fishermen regard it as a significant problem.

Nothing is known of the extent to which the sockeye re-enter the fishery once they have passed the fishing boundary, which at present is located approximately six miles below the head of the inlet. Reports have been received that when a net is set on the boundary, more fish are gilled facing down the inlet than

facing the closed area at the head of the inlet. Eventually, however, the escape-ment enters the Wannock River and proceeds upstream to Owikeno Lake where the fish spend some time before spawning. Some return downstream to spawn in the Wannock River, but the majority move up into the several spawning tributaries.

HAZARDS ENCOUNTERED DURING THE LIFE CYCLE

EGG LOSSES

Upon being expressed from the female, the egg must be fertilized and buried in the gravel. Since there does not appear to be any lack of male sockeye, it is unlikely that lack of fertilization would cause any major loss. Burial of the eggs and keeping them buried is definitely a source of some loss in the area. Areas of hard bottom in which the salmon are unable to bury their eggs are not extensive in this region, and tend to be used only when large populations occupy the better gravel, forcing some fish into the marginal areas.

Eggs, once buried in the gravel, may be uncovered either by being dug up by later spawning salmon (superimposition of redds), or by scouring due to freshets in the streams. When there is a heavy spawning population the former hazard undoubtedly causes losses in some of the streams, but it is not known whether these are serious. That scouring can cause serious losses is well known and this is always a great potential danger in a steep terrain. On the other hand, the extremely precipitous relief in the Owikeno area actually reduces scouring, in two ways. Firstly, the exceedingly rapid rise of the streams during freshets causes them to overflow into auxiliary channels, thus reducing the scouring in the main stream. (This involves a potential danger, that the stream may not return to its original channel when the flood subsides.) Secondly, the exceedingly rapid run-off into the lake results in correspondingly rapid fluctuations in lake level (the lake has been known to rise 5 feet overnight), and this in turn backs water up over the lower redds on many of the streams, reducing the current and preventing scouring over the flooded part of the spawning grounds.

The spawning areas protected by these means are limited. One factor tends to intensify scouring on the smaller streams in this area, and while this scouring may not directly remove eggs its effect may be just as serious. Since the area has not been logged, huge trees grow in the valley bottoms. Those alongside the streams tend to be undermined by scouring, eventually falling and generally tearing up large amounts of soil with their roots as they fall. The streams scour out the area thus loosened, particularly since the tree generally falls across and partially blocks the stream. Eggs may be lost in these cases from being smothered due to the deposition of debris in the gravel downstream from the scouring or from being deprived of oxygen due to a shift in the stream bed. Even when the eggs survive, the fry may be deprived of an outlet to the lake in the spring and thus be lost.

Animals which eat sockeye eggs in this area are probably better described as scavengers than predators. Exceedingly large numbers of birds, especially terns, may often be seen off the mouths of the spawning streams along the lake, and

near the redds. These birds are undoubtedly eating salmon eggs, but the eggs which they are able to obtain are mostly those which have been dug out of the redds by the agencies mentioned above. Other animals such as fish and insects also eat the exposed eggs. Certain animals which contribute to the loss of eggs are primarily predators on adult salmon, and will be discussed later.

Nothing is known of the extent to which low water, frost and snow cover during winter may cause mortality of eggs in this area.

FRY, FINGERLING AND SMOLT LOSSES

With their emergence from the gravel, predation may reasonably be expected to be the major factor in causing losses among the sockeye fry. Very little is known of the actual conditions which they encounter. However, from the fact that most of Owikeno Lake is glacially silted, and from Gilbert's observation that the yearlings grow very little in their first year, it is presumed that food is relatively scarce and/or hard to locate. There are indications that predators are also relatively scarce and it is probable that they have difficulty in locating their food, the sockeye, in the silted water.

Gilbert (1915) found that in their second season of scale growth, the sockeye grew rapidly, often adding as many circuli to the scale before migrating from the lake as were formed up to the time of the first annulus. Caution in interpreting this observation is necessary until it is determined exactly when the annulus is formed on these fish. If the annulus is formed at the end of winter, as is usually assumed, rapid spring growth may reflect increased production or availability of food resulting from the greater clarity of the lake in the early spring. Possibly, however, the annulus could be formed in the late summer or autumn when the silt content of the lake is high, and some of the growth after formation of the annulus takes place over the winter season. As mentioned previously, the yearling migrants leave the lake in May and June.

LOSSES AMONG ADULT SOCKEYE

Once the adult sockeye have entered the lake, there are relatively few factors known to contribute to further losses before they actually migrate to the redds. Harbour seals follow the run and are observed in the lake off the mouths of the spawning streams. The number of seals and the number of salmon taken by each is not known.

When the salmon enter the shallow water over the redds, the number of predators is increased. Though the most noticeable predators on the redds are bears, other animals such as eagles and wolves also take occasional fish. With regard to the bears, which in this region are mostly grizzlies, they appear to wholly consume those salmon which they obtain at the beginning of the run. As the run progresses, the spawned out salmon are much easier to catch, and being presumably less tasty, the bear is more inclined to take one or two bites or perhaps scorn the fish entirely after having caught it. Towards the end of the run, the bears apparently become fascinated by the sport of catching the fish, often making piles of salmon near favourite fishing spots. It is not known whether

this is done by all bears or, as would seem more likely, by cubs and yearlings. It certainly is not done because of hunger since often only one or two of the salmon will have even one bite taken out of them. I have examined large numbers of these salmon, and incompletely spawned fish are seldom found in the piles: nearly all are spawned out. This abundant evidence of bear predation is thus deceptive in that it is relatively harmless, while those salmon consumed green are usually marked by only a few opercular plates on a trail in the bush, and are very apt to be completely overlooked.

GLACIAL SILT AND ITS EFFECT ON THE SOCKEYE OF THE OWIKENO AREA

Since a great deal of the water which enters Owikeno Lake is melt-water from the many glaciers in the Owikeno drainage area, the lake contains large quantities of glacial silt. This silt is present in the whole of the lake below the outlet of the Shumahalt River, that is, about 95% of the total area. Above the Shumahalt, the Cheo River carries some glacial silt but it is not in sufficient quantity to have a noticeable effect much beyond the mouth of the stream.

Both the Shumahalt and the Machmell Rivers, though responsible for the extreme opacity of Owikeno Lake due to the huge quantities of glacial silt which they pour into the lake every summer, have nevertheless individually been mentioned as having quite large numbers of spawning sockeye in one or more years in the past. This is despite the fact that it is well known that silt can quickly cut off the oxygen supply and kill the eggs by stopping the flow of water through the gravel. There are several possible explanations. The fish in these streams might be strays from other areas, but this seems unlikely: the runs persist to these streams, though it is only occasionally that conditions are such that the fish can be seen clearly enough for estimates to be made. A second explanation is that the fish in these streams spawn in their clear tributaries, or just off the mouths of clear tributaries. This has been observed, but the small area of available gravel of this type, the large number of sockeye and their distribution in the river in those years when they could be seen, are decidedly against this explanation.

My own suggestion is that these fish normally spawn when the silt content of the glacial streams is being reduced by freezing on the mountains. Then when the gravel is disturbed by redd-making the current will remove silt and very little will be deposited. Also, as October, November and December are normally times of heavy rainfall in this area, a large addition of silt-free water tends further to flush and clean the redds. In the spring, the sockeye fry normally emerge before the glaciers begin melting, so that the fry escape from the gravel and are free swimming before any heavy deposition of silt again takes place. This hypothesis is at present unsupported by direct observations, but it appears to be a reasonable explanation of the situation.

It is not only in the redds that glacial silt will affect the sockeye, since it is very unlikely that all the Owikeno fry make their way to the clear five percent of the lake. It is well known that cold, deep, glacially-silted lakes are usually low

in basic organic production. The slow growth of Owikeno sockeye fingerlings was described above, but of course it may reflect the unusually large population as well as the physical conditions of the lake.

An advantage of the highly silted condition of the lake might be relative freedom from predation, because trout, char, etc., would not find it easy to locate the young sockeye.

Silt from the Owikeno drainage area is evident not only in the fresh water, but can be seen for several miles down the Inlet. Here the silt is chiefly in the surface layer of comparatively fresh water, overlying salt water below.

MANAGEMENT PROBLEMS

The survey of the Rivers Inlet sockeye has revealed a number of management problems in the area—some of them common to many sockeye nurseries, others of particular importance here.

1. EFFECT OF GILL-NET SELECTIVITY UPON PRODUCTION. Comparisons of commercial catches and spawning ground samples has shown that the smaller 4₂ sockeye, the larger 5₂'s, and all of the 3₂'s, are at a great advantage in escaping capture, and contribute disproportionately to the reproductive stock. The analyses of Milne (1955) and Godfrey (1958) have confirmed my long-held opinion that age at maturity in sockeye is in large part hereditarily determined, possibly entirely so. Accordingly it is not surprising to find (Godfrey, 1958, p. 346) that in the catch the average size of the 4₂ sockeye has decreased by about 1 pound, while the size of 5₂ sockeye has apparently increased by about half a pound, over the 45 years that the fishery has been sampled. This presumably reflects an increase in relative abundance of the *extremes* of size of the two fished age-groups in the stock. There is no way of knowing whether the relative number of the unexploited 3₂'s has also progressively increased over the years. Against the artificial selective advantage in survival which they enjoy must be set the opinion, held by some observers, that the small 3₂ sockeye are relatively ineffective in spawning situations when other males are present.

The increasing difference in size between 4₂ and 5₂ sockeye may be nothing more than a minor economic disadvantage (canning machinery functions best with fish of intermediate size); though it is also possible that the extremes of size have a smaller over-all productive potential than have average-sized fish⁴. Of more immediate practical importance is the fairly frequent occurrence of a substantial excess of females in the catch, and excess of males on the spawning grounds. This does not occur every year—the long-term average sex ratio in the catch is close to 50:50; but if closer control of the proportions of the sexes in

⁴Fisher (1930, p. 104) points out that natural selection must maintain the average magnitude of a continuously variable character, such as stature, close to the level which is biologically most effective in the prevailing environment; though of course *artificial* selection can alter such a character rapidly and drastically, as our domestic animals testify. Nylon gill-nets have been adopted in the sockeye fishery since the time of the 1952 comparisons shown in Figures 6 to 8, and these may have relaxed somewhat the artificial selection pressure against intermediate-sized fish.

the catch could be achieved, an appreciable addition to the catch would be possible in some years. In fact, it is not yet known that 50% males on the spawning grounds are necessary, or even desirable, and best utilization might involve taking more males than females every year.

2. SIZE OF SMOLTS. The average size of Owikeno smolts is so small as to raise the question whether some parts of the lake are not actually overstocked with fry. In general, very small smolts are associated with dense populations, and by any standard, Owikeno must contain a dense sockeye population. However Owikeno is also colder in summer than many sockeye lakes, and much siltier than most, and these factors may also contribute to the poor growth of the fingerlings.

It is well established that the smaller smolts of a run do not produce as many adult sockeye as the larger ones. This was deduced first from the observations that the average diameter (or the average number of circuli) from focus to annulus of yearling sockeye smolt scales is commonly less than that of adults of the same year-class when they return at ages 3₂, 4₂ or 5₂ (for examples, see Clutter and Whitesel, 1956, table 30). There has also been a direct measurement of the superior survival of smolts of larger sizes, by comparing runs in different years at Cultus Lake (Foerster, 1954). A short extrapolation of the Cultus Lake trend suggests that smolts as small as 2 g. would have only about a 2% survival rate (catch plus escapement) there, as compared with 10% for average-size smolts of 6 or 7 g. Of course, greater size and greater marine survival means smaller numbers initially, and the exact point of balance where net adult yield is greatest has not been determined for any stock. There is however a real possibility (at present it is nothing more) that the Owikeno smolts are too small to give maximum sockeye production from the lake, and that restricting spawning and fry output somewhat might improve total adult production. Information bearing on this point will be afforded by the relatively light spawning run of 1957, particularly the size of the smolts which it produces and the number of adults which they produce, in comparison with years of normal or heavy spawning.

3. FERTILIZATION OF THE LAKE BY SPAWNERS. Plankton blooms follow sockeye spawning in Basins 3 and 4 of Owikeno Lake, indicating a contribution to lake fertility and hence possibly to the food supply for the young fish. It may be that the lake's good production is being maintained only by the annual transportation of substantial organic and mineral supplies up from the sea by spawners in excess of those actually needed for best fry production⁵. Information on this point is evidently needed. If a part of the spawning run of sockeye is useful mainly as fertilizer, some cheaper form of fertilization might well be substituted.

4. PREDATORS. While seals, bears and birds take numbers of adult sockeye and numbers of sockeye eggs, they do not seem to be a serious problem in relation

⁵It has been suggested that the progressive decline in sockeye productivity at Karluk Lake, Alaska, which followed 25 years of phenomenal yields there, may be a result of a progressive reduction in lake fertility, following reduction in sizes of spawning stocks, although the most recent report on the lake rejects this interpretation (Rounsefell, 1958).

to the large numbers of sockeye now present at Owikeno. However additional study of their activities seems warranted.

It is also doubtful whether fish predators are very important; no exploratory netting has been done in the lake, but angling gives an impression of a scarcity of trout and char, while squawfish are absent. The silt in the water may make predation on young sockeye difficult, and help to explain the lake's high sockeye production and poor trout production.

5. PROTECTION OF SPAWNING GROUNDS. In their lower reaches, the large rivers entering Owikeno Lake frequently change their courses. What is a good spawning channel this year may become dried up or silted next year. Several plans for conserving or improving spawning grounds have been suggested. Most of these would probably involve major construction and maintenance costs, because of the large flows and extreme fluctuations in water levels. For the present, until it is determined whether the various parts of the lake need more fry or fewer fry, a conservative policy would be to maintain spawning conditions as they are now—without prejudice to future development works if they prove desirable. If an exceptionally good spawning area is currently threatened by the shifting of river channels, measures could be taken to preserve it if at all possible.

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Comparisons of the Index of Return for Several Stocks of British Columbia Salmon to Study Variations in Survival¹

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ABSTRACT

The "index of return" (ratio of offspring catch to parent catch) was used to compare annual survival among several stocks of British Columbia salmon. Over a period of almost 30 years the major stocks of pink salmon in the Province, excepting those of the Fraser River, exhibited quite similar annual variations in survival. The Fraser River stock behaved somewhat independently of the other stocks. There are indications that among pink salmon early ocean survival, probably during residence in estuarial and inshore waters, has played a major role in determining the level of final ocean survival. Among pink and sockeye salmon that entered the sea in the same year there is some similarity in early ocean survival. The latter relationship, if confirmed, may become useful for predicting sockeye ocean survival one or two years before the adult fish return.

INTRODUCTION

THREE CONSIDERATIONS have been of particular importance in defining management policies for the British Columbia salmon stocks and their dependent fisheries. These are (a) that freshwater mortality, from the time the eggs are deposited until the young are discharged into the sea, is high and variable; (b) that the magnitude of the spawning stock plays a large part in determining the abundance of young and, eventually, of adult fish; (c) that the ocean environment, and survival in the ocean, are relatively stable as compared with the freshwater environment and survival there.

In more recent years, however, as improvement in the management and conservation of these resources has grown, the need has grown, too, to develop more reliable means of predicting the abundance of the returning adult fish. Although, in the past, estimates of the final production in fresh water have been used for this purpose, they have often been fallible, and cannot be considered a sure basis for predicting the final production from the sea.

Furthermore, in terms of the marine life of the salmon, it has become evident that the ocean does not constitute a particularly stable environment from year to year. There is, perhaps, some justification for ascribing such constancy to the great ocean expanse, but certainly not to the coastal inlets so prominent in British Columbia, nor even to its inshore waters. These latter experience marked annual changes, brought about, mainly, through the action of such forces as deep-water upwelling, the tides, currents, winds, and the heavy and variable run-off of fresh water from the land. Significantly, it is these waters which first receive the young fish, and which provide their habitat during the early weeks, or even months, before they reach the open seas.

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In consideration of the possible effects of such a variable environment upon the salmon in the sea it has become increasingly desirable to learn more of their life history during the ocean phase. The present study was carried out as part of a general examination of available data aimed at providing a background of information that would be useful in setting up a program to investigate the survival, growth and dispersal of the young fish during their early residence in coastal waters.

The "index of return" used in this paper is defined as the ratio of the catch of offspring fish to the catch of parent fish. Within the limits of error that occur through deviation of the catch from a constant fraction of the total adult return (catch plus escapement), the index is a measure of the success of a parent stock in producing adult offspring.² Fluctuations in the magnitude of the "index of return" will reflect annual variations in the survival of broods. Also, since the index is computed from two generations of adult fish, it is a measure of over-all survival, including both the freshwater and ocean phases.

Among most fishes mortalities are highest and most variable during the early life stages, when they are smallest, most fragile and most vulnerable to the various environmental stresses. This corresponds among pink and chum salmon, once they have become free-swimming forms, to the period following emergence from the gravel and the downstream migration and early residence in estuarial waters; among sockeye salmon it corresponds to the period of their migration to the lake and residence there. With pinks and chums, therefore, variations in early ocean survival are likely to have a greater relative effect in determining total survival than in the case of sockeye salmon. Conversely, the same might be expected of sockeye salmon in respect of variation in freshwater (especially lake) survival.

In the following analyses comparisons have been made between several stocks of pink salmon, mainly with a view to determining whether their survival histories, as indicated by annual changes in the "index of return", have been similar or dissimilar. Also, those years are identified in which survival among stocks originating over a wide geographic range were particularly good or poor, with the expectation that it may be possible later to indicate the outstanding environmental features associated with such years.

Similar comparisons between stocks of chum salmon were also attempted. However, these fish mature at a variable age (in their third, fourth or fifth year of life), and since age of return data were not available, the "index of return" could not be calculated, because it was not possible to compute correctly production from parent stocks.

Several estimates of ocean survival for pink salmon, based upon fry output to adult return, were compared with the pink salmon "index of return" computed in the usual manner. These analyses were done in order to assess the importance of the inshore ocean environment in determining the final survival from the sea.

²A similar index has been used by several workers in the past for sockeye salmon, and by Hoar (1951) for pink and chum salmon.

Comparisons between pink and sockeye salmon have been made in two ways: first, between the "index of return" for both species; and, second, between the index for pink salmon and estimates of sockeye ocean survival computed from smolt output and adult return. In each case comparisons were between fish that had entered the sea in the same year. The purpose here was to determine whether the two species might be similarly affected to some degree by the environmental conditions of inshore waters, which for a period both encounter together.

As a measure of total survival the "index of return" is subject to considerable error at times, mainly because fishing intensity does vary from year to year. However, in these analyses the writer has been concerned more with certain generalizations regarding the British Columbia salmon stocks as a whole, rather than with specific stocks or particular events. I have attempted to relieve the effect of this sort of error somewhat by grouping index values into several broad categories. Workers interested in the survival of certain individual stocks in particular years should whenever possible refine the index by including accurate escapement data.

METHOD

The "index of return" (which will be referred hereafter as the I.R.) is computed as a percentage as:

$$100 \times O/P,$$

where O = catch of offspring fish, and P = catch of parent fish. For some comparisons the I.R.'s have been grouped into 5 categories: Excellent (E); High (H); Normal or Average (N); Low (L); and Poor (P). After converting the I.R.'s to logarithms, these categories are such that the intervals between them are approximately equally spaced, as follows:

- E: 2.17+ (150% and greater)
- H: 2.05 to 2.17 (114-150%)
- N: 1.94 to 2.05 (88-114%)
- L: 1.83 to 1.94 (67-88%)
- P: 1.83- (67% and less)

Comparisons have been made between different stocks (i.e., catches in different fishing areas) of the same species for the same years; and between different species for the same years in the same area. In two instances I.R.'s have been compared with estimates of ocean survival based upon the output of young fish to the sea and the subsequent return of adult fish. Further details of treatment of data are given as necessary along with the results.

In the case of pink salmon, I.R.'s were computed using an invariable 2-year age of return (since known exceptions to that age are extremely rare). For sockeye salmon a 4-year age of return was used for Fraser River fish (since they invariably constitute the great bulk of returning adults), and 4- and 5-year ages for Skeena River and Rivers Inlet fish (since together these ages constitute about 90% of the mature fish in those areas). For these two fisheries age composition of catches was necessary, and was available as described below.

In two instances catches in adjacent fishing areas were combined in order to compute I.R.'s for the resulting larger areas. These were the combined areas of Nass-Skeena-Central and Rivers-Smith. This was done in the event that mixed stocks of fish passed over the fishing grounds, so that catches in any one area might include fish of adjacent areas, in which case assignment to area of origin would be incorrect.

Data used in these analyses were obtained from the following sources.

Pink salmon packs in British Columbia from annual reports of the Provincial Department of Fisheries; in Alaska, from the Pacific Fisherman Yearbook.

Fraser River pink salmon I.R.'s were based upon combined Canadian packs and packs of fish caught in Puget Sound, as recorded in the Pacific Fisherman Yearbook.

In the comparison of pink salmon I.R.'s in British Columbia Fisheries Statistical Areas 5 to 10, inclusive, computations were based upon catch figures (in numbers of fish) given in the British Columbia Catch Statistics, Department of Fisheries of Canada, 1951-1957.

Skeena River and Rivers Inlet sockeye salmon I.R.'s were computed from estimated numbers of 4- and 5-year-old fish, such estimates being determined from annual packs, using age composition data and adjusting for weight differences between the two age groups (Godfrey, 1958).

Fraser River sockeye I.R.'s were from combined United States and Canadian packs, as published in the Washington State Department of Fisheries, Commercial Fishing Statistics.

The present fisheries statistical areas of the Province are outlined in Fig. 1. The areas used in the annual reports of the Provincial Department of Fisheries (the principal source of data for computing I.R.'s) would include areas shown in Fig. 1 approximately as follows:

Queen Charlotte Islands	Areas 1 and 2
Nass River	Area 3
Skeena River	Area 4
Central Area	Areas 5-8 inclusive
Rivers Inlet	Area 9
Smith Inlet	Area 10
Vancouver Island District and adjacent mainland	Areas 11-27 inclusive
Fraser River	Areas 28 and 29

RESULTS

PINK SALMON

COMPARISONS BETWEEN STOCKS. Pink salmon I.R.'s for the (parent) years 1927 to 1954 for 12 areas are listed in Table I and are compared in Fig. 2. The shaded portions in the graphs enclose the years in which I.R.'s were below the replacement level of 100%—that is, when the offspring catch was smaller than the parent catch.

Several of the 12 areas have experienced similar variations in survival rates in the same years or groups of years. For example, periods such as 1929-30, 1933-35, 1943-45 and 1950-52 include one or more years of poor survival for most areas; and periods such as 1931-32, 1936-37, 1941-43 and 1946-49 include one or more years of good survival for most areas.

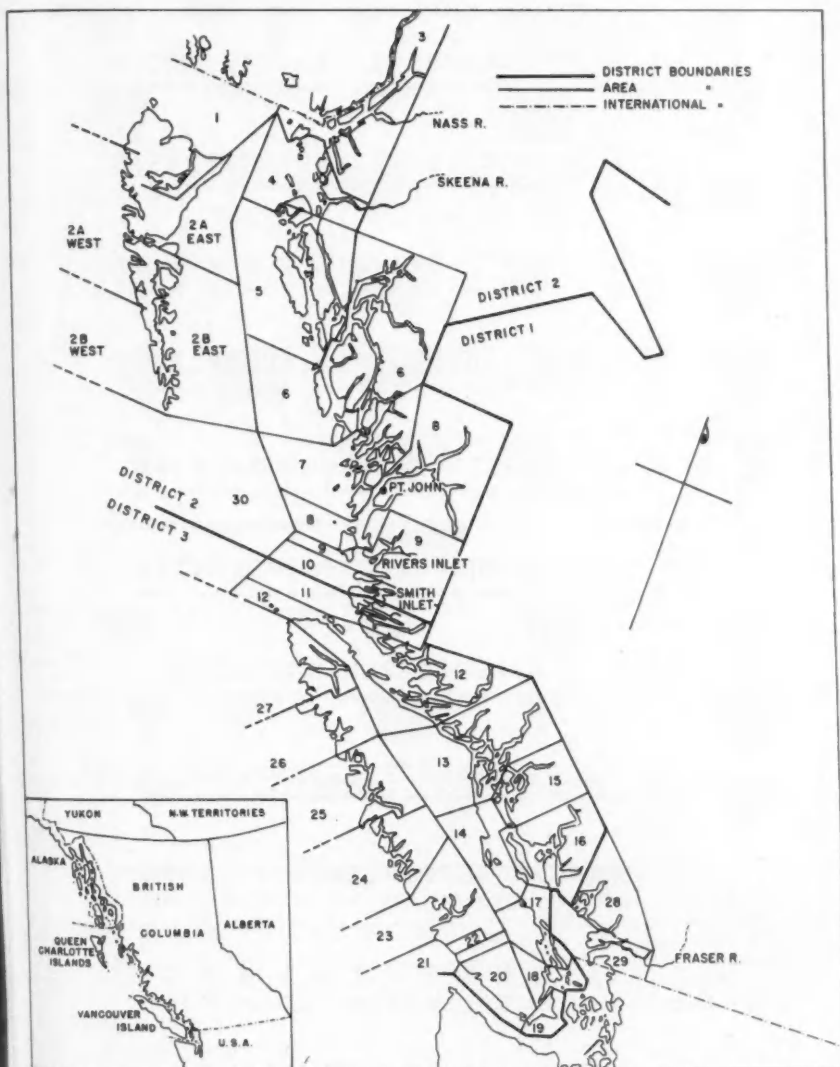


Fig. 1. Present statistical areas for British Columbia fisheries.

TABLE I. Log₁₀ values of pink salmon I.R.'s computed from data contained in sources described in the text, p. 894.

Parent year	Q.C.I.	Nass	Skeena	Central	Rivers	Smith	Van. I.	Fraser	Central Alaska	S.E. Alaska	Nass Central	Rivers Smith
1927	...	1.79	2.39	...	2.55	2.07	2.15	2.11	2.09	2.42	2.28	2.36
1928	...	1.98	2.12	...	2.04	3.00	2.33	...	2.11	2.03	2.08	2.32
1929	...	1.70	1.67	...	2.33	1.99	2.05	1.91	1.96	2.12	1.67	2.26
1930	...	1.75	1.32	...	1.28	0.85	1.57	...	1.93	1.78	1.71	1.11
1931	...	2.93	2.33	...	2.00	2.38	2.32	1.94	1.88	1.86	2.68	2.63
1932	2.34	1.86	2.34	2.29	1.91	2.78	2.21	...	2.22	2.28	2.24	2.32
1933	...	1.93	1.93	1.97	1.95	1.34	2.05	1.88	2.17	2.18	1.92	1.56
1934	2.22	2.36	1.86	2.20	2.36	0.95	2.18	...	2.12	2.05	2.12	1.83
1935	...	1.49	1.86	2.01	2.22	1.04	2.22	1.94	2.15	1.99	1.91	1.95
1936	1.81	1.91	1.88	1.72	2.15	2.43	1.93	...	1.92	1.81	1.80	2.22
1937	...	2.52	2.20	2.19	2.20	2.92	1.87	1.95	1.85	1.84	2.22	2.30
1938	1.89	1.68	1.83	1.62	1.57	1.63	1.68	...	2.03	1.88	1.70	1.58
1939	...	1.93	1.72	1.64	1.60	1.28	1.87	1.83	1.99	2.39	1.71	1.54
1940	2.27	2.22	2.05	2.10	1.46	1.85	1.63	...	1.86	2.08	2.12	1.56
1941	...	1.89	2.03	2.64	2.24	1.87	1.87	1.56	2.10	1.46	2.41	2.20
1942	2.04	1.81	1.97	2.37	2.74	1.98	2.53	...	1.98	1.79	2.15	2.59
1943	...	2.31	2.11	2.10	2.08	2.63	2.27	2.64	1.97	2.00	2.11	2.14
1944	0.90	1.38	1.34	1.70	1.49	1.67	1.11	...	2.02	1.96	1.61	1.51
1945	...	1.15	1.28	1.45	1.96	1.65	2.17	2.27	1.93	1.81	1.54	1.91
1946	2.81	2.08	2.67	2.27	2.91	1.80	2.81	...	1.77	1.83	2.33	2.90
1947	...	2.83	2.40	2.23	2.12	2.38	2.01	1.92	1.75	2.49	2.16	2.16
1948	2.26	1.72	1.72	2.03	1.98	2.55	2.48	...	1.96	1.89	1.98	2.08
1949	...	2.32	1.96	2.14	2.25	1.99	1.92	1.91	1.76	1.76	2.15	2.21
1950	2.28	2.01	2.53	2.10	1.99	2.09	2.11	...	2.01	2.05	2.18	2.02
1951	...	1.36	1.99	1.59	1.54	1.61	2.16	2.10	2.26	1.46	1.61	1.54
1952	1.77	2.45	1.64	1.76	1.32	0.90	1.28	...	2.03	1.94	1.80	1.20
1953	...	2.24	2.46	...	2.08	2.35	1.98	1.95	2.08	2.19	2.23	2.12
1954	1.92	2.08

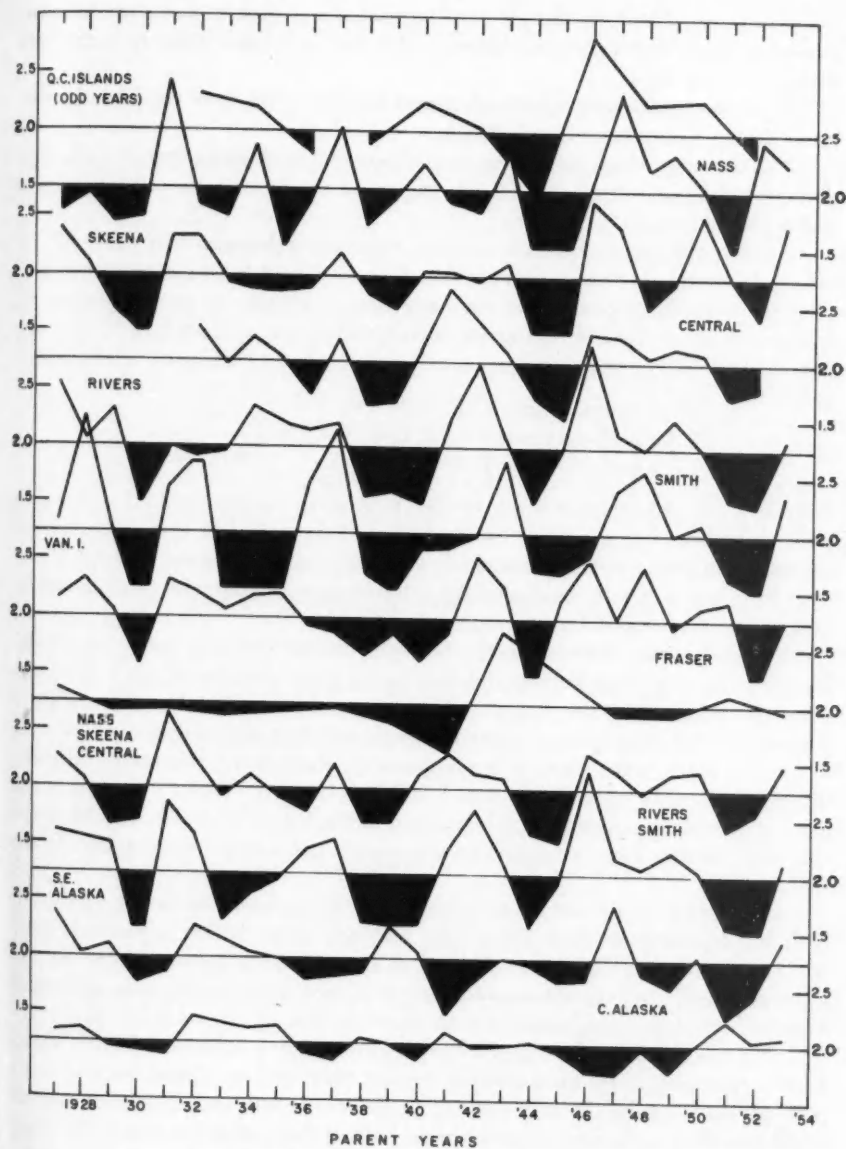


FIG. 2. Comparisons of \log_{10} I.R. values for pink salmon of 12 areas.

The Queen Charlotte Islands have large stocks of pink salmon only in even-numbered years, and agreement between this and most other areas in such years is also relatively high.

There is particularly good agreement between the two combined areas, Nass-Skeena-Central and Rivers-Smith.

The one area which has shown least agreement with other British Columbia areas is the Fraser River (which has important stocks of pink salmon only in odd-numbered years).

A more detailed comparison between these several stocks may be made by especially considering those years in which survival had been either particularly good or particularly poor. This has been done for each of any two areas by grouping their coded I.R. values for corresponding years according to whether they showed "agreement", "disagreement", or a "neutral (indefinite) relationship", as follows:

I.R.'s in agreement—E-E; E-H; P-P; P-L.

I.R.'s in disagreement—E-P; H-P; E-L; H-L.

I.R.'s neutral—N-N; H-N; L-N; H-H; L-L; N-E; N-P.

(It might be argued that some of the neutral groupings could be included with either those that agreed or those that disagreed; but then the test for identification with years of *particularly* good or *particularly* poor survival would have been less stringent. Undoubtedly, other groupings might be feasible and of interest for somewhat different purposes.)

Table II shows the results of such comparisons between each pair of the 12 areas. The first point of interest is that in the great majority of cases there was more agreement than disagreement. Excepting only the Nass-Vancouver Island comparison, the only cases of more disagreement than agreement were all with the Fraser River area. Here, in 6 comparisons, there were 5 instances of more disagreement than agreement, and 1 instance (Skeena-Fraser) in which the percentages of agreement and disagreement were equal. It should also be noted that in the Fraser River comparisons the neutral percentages were generally not high.

In some instances, but by no means invariably, there was better agreement between adjoining or close areas than between areas farther separated, thus:

(a) The Queen Charlotte Islands area showed much agreement and no disagreement with the Nass-Skeena-Central area, but considerably less agreement together with some disagreement with the more distant Rivers-Smith area.

The Queen Charlotte Islands-Vancouver Island comparison, which shows much agreement, is for even-numbered years only, and is related mainly to the pink salmon stocks on the west coast of Vancouver Island, and at the northern tip of the Island in particular, since the great bulk of them originate there. (In even-numbered years Vancouver Island pink catches are mainly of west-coast origin; and, as mentioned earlier, the large stocks of Queen Charlotte Island pinks occur in the even-numbered years only.)

(b) Agreement with the Central area decreased progressively southwards; that is, in the order Rivers Inlet, Smith Inlet, Vancouver Island and Fraser River.

Although the percentage agreement between the Central area and the Skeena was less than between the former and the Nass (55% as compared with 64%), the percentage disagreement was much less in the Central-Skeena comparison (4% as compared with 18%); also, the neutral percentage was high for the Skeena (41%) and much lower for the Nass (18%).

(c) The two combined areas Nass-Skeena-Central and Rivers-Smith, which showed considerable agreement and relatively little disagreement, are adjacent.

With the exception of two years in particular (1939 and 1951), the two Alaskan areas also showed much similarity.

From these comparisons it appears reasonable to conclude that over a period of almost 30 years the major stocks of pink salmon, from areas of origin covering a wide geographic range along this coast, have shown considerable agreement in their variations in annual survival rates, notably, perhaps, in years of especially good or especially poor survival. In general, the Fraser River pinks appear to have behaved somewhat independently of the other British Columbia stocks.

It may be inferred from this that most of these stocks had simultaneously experienced certain environmental conditions (either freshwater or marine, or both) that had similarly determined their reproductive success. It seems that this could only be the result of some wide-ranging climatic factor or factors, which would affect both spawning streams and coastal waters.

The deviation of the Fraser River from the general situation common to other British Columbia areas, if it is real, may possibly be the result of differences in early oceanic experiences rather than different freshwater experiences. It is difficult to conceive that the climate affecting the spawning areas of the Fraser pink salmon (which, unlike the sockeye, have been mainly in the lower river since 1915) would be markedly at variance with the climate of areas farther north. However, that is not certain; in any event, the most pertinent feature of the early oceanic experience of the Fraser stocks would be the Fraser River itself, and its influence over a wide expanse of inshore waters.

YEARS OF EXCEPTIONAL SURVIVAL. In Table III coded I.R.'s for the 12 areas are listed by parent and by first sea-year. Both years are given since in either or both might have occurred the environmental events which were mainly responsible for the annual variation in survival rates.

In British Columbia, but excluding the Fraser River, years of especially good or poor survival were selected, as shown below, on the basis that most areas had very high or very low I.R. values, respectively. The figures in brackets refer to the first sea-years.

Good years: 1931(32), 1932(33), 1934(35), 1937(38), 1943(44), 1946(47), 1947(48), 1953(54).

Poor years: 1930(31), 1936(37), 1938(39), 1939(40), 1944(45), 1945(46), 1951(52), 1952(53).

There were only three exceptional (i.e., with E or P values) years for the Fraser River, viz. Good-1943(44), 1945(46), and Poor-1941(42).

COMPARISON OF I.R.'S WITH KNOWN OCEAN SURVIVAL RATES. Ocean survival rates can be computed from known numbers of seaward migrating fry and known numbers of returning adults. Usually it is not possible to determine how many fish of a specific stock were taken in the fishery, so that survival rates are based only upon the adults that return to the spawning grounds. Such survival rates include the effects of both fishing and natural ocean mortality, and err in relation to one another, between years, as a relative measure of natural ocean mortality, if fishing mortality varies from year to year. The "index of return", on the other hand, is computed from catches only, and as a relative measure of ocean mortality it therefore errs according to the deviation of the catch from a constant fraction of the total adult return. Within these limits, however, comparisons of I.R.'s with known ocean survival rates are useful in permitting more definite statements to be made regarding the use of the "index of return" as a measure of variation in ocean survival.

Ocean survival rates, computed from known numbers of fry migrants and adults returning to Hooknose Creek, British Columbia, are available for several years (FRB, 1956, 1957, and subsequent unpublished figures; data collected by J. G. Hunter). In Table IV they are compared by parent year with I.R.'s calculated for pink salmon catches in Statistical Area 8, in which Hooknose Creek is situated.

TABLE IV. Comparison of Hooknose Creek pink salmon ocean survival estimates with I.R.'s for pink salmon of Area 8.

Parent year	Area 8 I.R.	Percentage survival Hooknose Creek
1951	1.64(P)	0.7
1952	2.12(H)	2.6
1953	1.53(P)	0.6
1954	2.08(H)	2.4
1955	2.28(E)	2.7

Agreement is relatively high. Since the survival rates are quite independent of events that occurred during the freshwater period, and since the I.R.'s show such close agreement with them, it follows that the variation in the I.R.'s must have been determined to a great extent by annual changes in ocean survival, brought about by changes in the ocean environment.

The low survival from the 1953 parent stock occurred not only to the pinks of Hooknose Creek, but to pinks of Area 8 as a whole, which includes several important streams and large stocks of these fish. However, this situation was in marked contrast to the good survival in the same year in the adjacent areas of 5, 6, 7, 9 and 10.

There have been other years in which the survival of pinks in Area 8 has differed significantly from that in the adjacent areas north and south of it. This situation is particularly interesting, therefore, because it strongly suggests that

the survival of pink salmon during their ocean residence must be determined mainly at an early period, when they are in inshore waters.

The numbers of pink salmon caught in Areas 5 to 10 are available for the years 1951 to 1957. Comparisons of I.R.'s computed from these catches are shown in Table V. There it can be seen that for the five available (first sea) years of 1952 to 1956, there was very close agreement and no disagreement between each of Areas 5, 6, 7, 9 and 10, but that Area 8 agreed with the other areas only twice (in 1952 and 1955), and disagreed on three occasions (in 1953, 1954 and 1956).

TABLE V. Comparison of pink salmon I.R.'s for Areas 5 to 10.

1st sea year	Areas					
	5	6	7	8	9	10
1952	P	P	P	P	P	P
1953	P	P	L	H	P	P
1954	E	E	E	P	N	H
1955	E	E	E	H	E	E
1956	P	P	P	E	P	P

This deviation of Area 8 from the situation common to the areas adjacent to it would appear to be possible only if the rate of ocean mortality had already been mainly determined in inshore waters, before the young fish had reached the waters of Queen Charlotte Sound and Hecate Strait. In the latter, oceanic conditions are probably relatively uniform throughout, so that it might be expected that once they had entered these waters, the fish from all six areas would be similarly affected by the conditions they would encounter there.

COMPARISONS BETWEEN PINK AND SOCKEYE SALMON

COMPARISONS BASED UPON OUTPUT OF SOCKEYE SMOLTS. Babine Lake produces 75% or better of the Skeena River sockeye, and estimates of the output of sockeye smolts from that lake are available for four years (FRB, 1957 and subsequent unpublished figures; data collected by F. C. Withler and K. V. Aro). Ocean survival rates for Skeena sockeye have been computed using these smolt estimates and the resultant catches of 4- and 5-year-old sockeye taken in the Skeena fishery (in Statistical Area 4). The great majority of Skeena sockeye are in their second year of life when they enter the sea; and 90% or more of adult Skeena sockeye are either 4- or 5-year-old fish. Thus, after entering the sea, survivors would return as mature fish either two (4-year-olds) or three (5-year-olds) years later.

The sockeye survival rates are compared with pink salmon I.R.'s for the Skeena area, comparisons being between fish that entered the sea in the same year. Both species leave the river and are present together in estuarine waters at approximately the same time of year, that is, during May to June approximately (Manzer, 1956).

The following tabulation compares the percentage survival rates for sockeye (smolts to returning adults in catch) with the pink salmon I.R.'s in their coded

form. Letters in brackets after the sockeye survival rates are coded values which are intended to correspond approximately to those for pinks. The years of adult sockeye return shown are for 4- and 5-year-old fish, respectively.

<i>1st sea year</i>	<i>Sockeye</i>	<i>Pinks</i>	<i>Years of adult sockeye return</i>
1951	2.91(E)	E	1953 and 1954
1952	1.08(N)	N	1954 and 1955
1953	0.34(P)	P	1955 and 1956
1954	2.29(E)	E	1956 and 1957
1955	?	P	1957 and 1958
1956	?	E	1958 and 1959

The agreement between the four available first sea years is good. A possible interpretation of the relationship is that, (a) the ocean survival of the two species is determined to a great extent by their early experiences in inshore waters; and (b) that to an important degree the two species are similarly affected by the environmental conditions they encounter in those waters, which for a period they inhabit together. (Manzer, 1956, has indicated that the seaward dispersal of the sockeye is more rapid than that of the pinks.)

If the above interpretation has some validity, the prognostication could be made that in 1958 a good survival of 4-year-old sockeye and a relatively low survival of 5-year-old sockeye in the Skeena fishery could be expected. At this time, however, the relationship has little statistical significance, because of the paucity of observations. It is at present sufficient to indicate the relationship and to state that if it does have a real biological basis, a useful tool for the prediction of sockeye survival may be available in the future.

COMPARISONS OF PINK AND SOCKEYE I.R.'s. Pink and sockeye salmon I.R.'s, both computed on the basis of parent catch to offspring catch, may be compared. The comparisons are between years in which pinks go to sea as fry and sockeye as year-old smolts (although some spend longer, the great majority of British Columbia sockeye spend one year in lake residence before making their seaward migration). Any agreement found can thus be attributed to similar variation in marine survival, since the oviposition and the hatching of the two species occurred in different calendar years. Of course, the I.R. basis of comparison between the two species, although it is more widely useful than the method used in the previous section, is much less discriminating.

Log₁₀ values of sockeye salmon I.R.'s for Skeena River, Rivers Inlet and Fraser River are given in Table VI; comparisons between the two species of these areas are shown in Table VII and Fig. 3.

In Fig. 3 there are definite indications of some similarity between species, even though they were frequently not in agreement in specific years. For example besides some similarity in over-all trends, the amplitudes of changes shown by the two species in the same area were more alike than between different areas.

TABLE VI. Log₁₀ values of sockeye salmon I.R.'s for Skeena River, Rivers Inlet and Fraser River; computed from data contained in sources described in text, p. 894.

Parent year	Skeena River	Rivers Inlet	Fraser River
1918	2.15
1920	1.99
1922	2.11
1924	1.92
1926	2.02	2.16	2.54
1927	1.88	2.01	...
1928	2.05	2.23	2.21
1929	1.67	1.86	...
1930	1.60	2.05	2.03
1931	1.81	2.13	...
1932	2.18	1.93	2.22
1933	1.98	2.16	...
1934	2.09	1.72	1.82
1935	2.10	1.63	...
1936	2.29	2.27	1.80
1937	2.12	2.13	...
1938	1.77	1.75	2.33
1939	1.87	1.33	...
1940	1.90	2.06	1.91
1941	1.88	1.98	...
1942	2.01	2.36	1.95
1943	1.90	1.67	...
1944	2.34	1.81	2.08
1945	1.71	2.20	...
1946	2.02	1.96	1.51
1947	2.20	1.75	...
1948	2.00	2.25	2.18
1949	2.00	2.39	...
1950	2.70

Statistically, the correlation between the I.R.'s for pinks and sockeye was significant at Rivers Inlet ($r = +0.476$; $P < 0.05$), but not significant at Skeena River ($r = -0.232$) and Fraser River ($r = +0.086$).

Table VII shows that on the basis of comparing similar years of especially good or especially poor survival (see p. 900), there was good agreement at Rivers Inlet, less for the Fraser, and little agreement together with much disagreement for the Skeena. The Rivers Inlet and Fraser River data warrant closer consideration.

RIVERS INLET: Corresponding to 9 E values for pinks were 4 E's, 3 H's, 1 N and only 1 directly opposite P value for sockeye; and against 5 P values for pinks were 3 P's, 1 L and only 1 opposite H value for sockeye; also corresponding to 5 E values for sockeye were 4 E's and 1 H for pinks; and against 7 P sockeye values were 3 P's, 2 N's, 1 H and 1 E for pinks.

There was, therefore, much similarity in considerable detail between extremes of marine survival of the two species at Rivers Inlet.

FRASER RIVER: Corresponding to 2 E's for pinks were N and H values for sockeye; and to 1 P for pinks was an L for sockeye; also, corresponding to 6 E's for sockeye were 2 H's and 4 L's for pinks; and to 3 P's for sockeye were 2 L's and 1 N for pinks.

At the Fraser River there was more agreement than disagreement between extremes of survival; also a large proportion of the years fall into the "neutral" category.

TABLE VII. Comparison between sockeye salmon and pink salmon I.R.'s for fish that entered the sea in the same year, for Skeena River, Rivers Inlet and Fraser River stocks.

1st sea year	Skeena River		Rivers Inlet		Fraser River	
	Pinks	Sockeye	Pinks	Sockeye	Pinks	Sockeye
1920	N	H
1922	H	N
1924	H	H
1926	N	L
1928	E	N	E	H	H	E
1929	H	L	N	N
1930	P	N	E	E	L	E
1931	P	P	P	L
1932	E	P	N	N	L	N
1933	E	P	L	H
1934	L	E	N	L	L	E
1935	L	N	E	H
1936	P	H	E	P	L	P
1937	L	H	H	P
1938	E	E	E	E	N	P
1939	L	H	P	H
1940	P	P	P	P	L	E
1941	N	L	P	P
1942	N	L	E	H	P	L
1943	N	L	E	N
1944	H	N	H	E	E	N
1945	P	L	P	P
1946	P	E	N	P	E	H
1947	E	P	E	E
1948	E	N	H	N	L	P
1949	P	E	N	P
1950	N	N	E	E	L	E
1951	E	N	N	E
1952	H	E
	No.	%	No.	%	No.	%
Agreement	4	17	12	50	6	35
Disagreement	10	41	4	17	4	24
Neutral	10	41	8	33	7	41

SUMMARY AND CONCLUSIONS

The "index of return", (ratio of offspring to parent catch, or I.R.) was used to compare variations in annual survival between certain stocks of British Columbia salmon.

Over a period of almost 30 years (1927 to 1954) pink salmon stocks from all major areas of the Province, excepting the Fraser River area, showed much agreement in their annual fluctuations of survival rates. The Fraser River area was the only British Columbia area which was often at variance with the general situation in any year or group of years.

Much similarity was found between pink salmon I.R.'s and pink salmon ocean survival estimates in one area for which data were available (Table IV). Since the latter are independent of earlier survival in fresh water, some importance can therefore be attached to the I.R. as a relative measure of annual changes in ocean survival, as distinct from total or freshwater survival. Furthermore, the

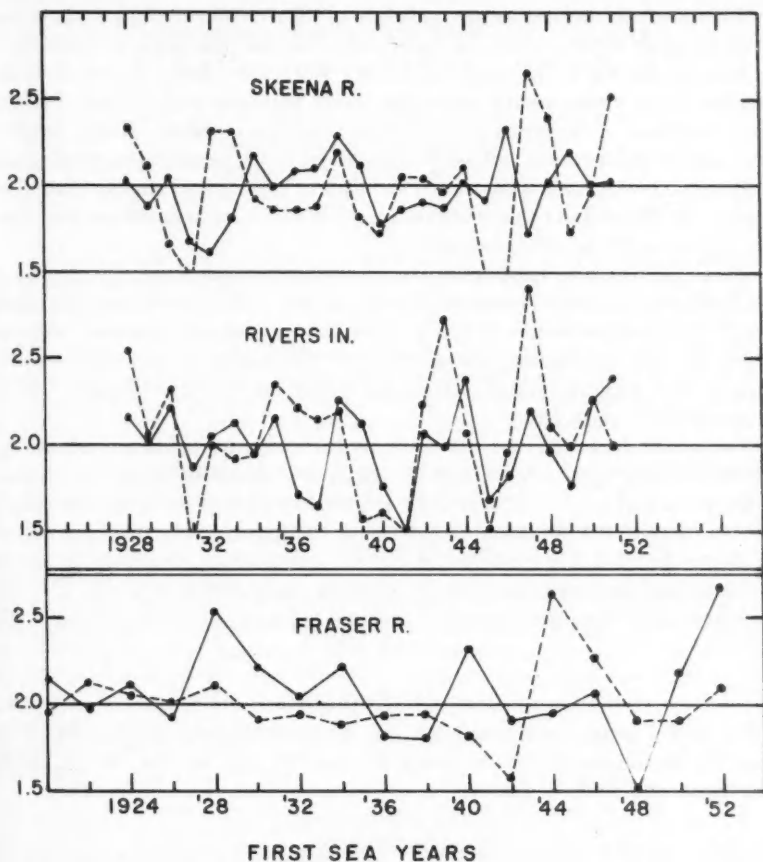


FIG. 3. Comparisons between pink and sockeye salmon \log_{10} I.R. values, for Skeena River, Rivers Inlet and Fraser River. Solid lines—sockeye; broken lines—pinks.

I.R.'s for this area, Statistical Area 8, differed markedly in 3 out of 5 years from the I.R.'s for the 5 adjacent areas north and south of it; these latter areas showed almost complete agreement between themselves in each of the 5 years. Since fish from all 6 areas eventually had to reach and pass through the waters of Queen Charlotte Sound or Hecate Strait, which probably have relatively uniform environmental conditions throughout, the different survival shown by Area 8 must have been associated with conditions in more inshore waters (in the inlets and estuaries). Thus among pink salmon, which migrate seaward immediately upon emergence from the gravel, early mortalities in estuarine and inshore waters when the fish are small are probably of principal importance in determining their final survival from the sea.

Estimates of sockeye ocean survival at Skeena River, based upon smolt output to adult return, were compared with Skeena pink salmon I.R.'s for fish that entered the sea in the same year. They were very similar for each of the 4 available years. Comparisons were also made between pink salmon I.R.'s and sockeye salmon I.R.'s, similarly computed, for Skeena River, Rivers Inlet and Fraser River. In each area, although specific years frequently disagreed, general trends of the two species were similar in years of extremes of survival rate (good or poor). At Rivers Inlet the relationship, using *all* years, was statistically significant, but not so at the other two areas.

These pink-sockeye relationships suggest that to some degree the two species have similar survival experiences during the period of their common habitation of estuarine and inshore waters. If this persists, the prior determination of the ocean survival of pink salmon may be of value in predicting the survival and adult return of the sockeye, which follow the pinks one (4-year-old fish) or two (5-year-old fish) years later.

The writer has used the "index of return" with no reference whatever to escapements, nor with any attempt to adjust for variations in fishing intensity. For the years and stocks involved such refinements of method were not possible. However, despite this weakness in the use of the index, it has still been possible to indicate the probable existence of certain relationships affecting the survival of salmon, and of particular interest, of their early ocean survival. The latter constitutes one of the more important unknown phases in the life history of these fishes.

ACKNOWLEDGMENTS

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Population Studies on Juvenile Herring in Barkley Sound, British Columbia^{1,2}

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ABSTRACT

Population studies were carried out on herring in the juvenile (first year, post-metamorphosis) stage in Barkley Sound in the summers of 1951 to 1954. Their chief objective was to detect and estimate yearly changes in relative abundance. The juveniles were found mostly in shallow, sheltered bays, inlets and channels, mainly on the southeast side of the sound. The stocks apparently arose from different mixtures of the progeny of a series of spawnings extending over two months and located mainly on the northwest side of the sound. Mixing between localities averaged less than one-third. The 1953 and 1954 juvenile populations were above average (both about 640 million fish), while the 1952 population was below average. Upon recruitment to the fishery, the relative strength of these three year-classes was comparable to that observed in the juvenile stage. Thus, surveys of herring abundance at the juvenile stage provide an index of year-class strength at recruitment.

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INTRODUCTION

THE PACIFIC HERRING, *Clupea pallasii* Valenciennes, goes through egg, larval, immature and adult stages. In southern British Columbia, the eggs are deposited on vegetation in the intertidal zone in late winter or early spring (mid-January to mid-April). They hatch in about 2 weeks (Stevenson, *et al.*, 1952) into larvae, which metamorphose in 6 to 8 weeks (Stevenson, 1955a) into the adult form. These young herring remain inshore until September or October, when they migrate offshore. During this inshore stage, the herring are referred to as juveniles. Except for rare inshore appearances of schools of second-year fish, older herring remain offshore until they join the spawning stocks as mature adults, usually in the third year (Stevenson, 1955b).

Appreciable fluctuations occur in the abundance of herring in British Columbia (Taylor, 1955, and previous reports in that series). Once a year-class

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enters the fishery (i.e. matures for the first time), its future strength may be predicted on the basis of fishing mortality and calculated rates of natural mortality (Tester, 1955). As these two factors do not appear to appreciably alter relative year-class strength from year to year, it must thus be established prior to maturity. Since the newly recruited year-class usually makes up more than half of the adult population in southern British Columbia stocks, it is both the major source of variation in population abundance and the key to the prediction of population size.

Considerable attention has been given to determining mortality in the early stages of the life history of the herring in British Columbia waters. Studies on egg mortality (Tester, 1948; Stevenson, 1952; McMynn and Hoar, 1953) give estimates of mortality varying from 35% to 65%, due mainly to bird predation. Losses due to other factors are small (less than 10%). A re-analysis of experimental data from these and other studies conducted at the Biological Station, Nanaimo, B.C., indicated a total mortality of about 79%. However, year-class strength has shown no correlation to the amount of spawn deposited (Tester, 1948). This is well illustrated by the exceptionally strong 1947 year-class on the west coast of Vancouver Island, which was produced from a lower-than-average spawning (Stevenson *et al.*, 1951) and the very poor 1940 year-class, which was produced from an above-average spawning (Tester, 1948).

Stevenson (1955a), on the other hand, has been able to establish a correlation between year-class strength and conditions affecting larval survival in Barkley Sound. On the basis of these data, and data on the amount of spawn deposited and the extent of mortality between metamorphosis and recruitment, he estimated mortality during the larval stage to be 99.3 to 99.7% (Stevenson, 1955b). He concluded that mortality during this vulnerable stage is the major factor involved in fluctuations in year-class strength. It would thus appear that the earliest stage in the development of the Pacific herring at which year-class strength may be assessed is that immediately following the larval stage—namely, as juveniles. Since the herring migrate offshore and scatter at the end of their first summer, the early juvenile stage is the last stage before recruitment at which they are relatively accessible for population studies.

THE BARKLEY SOUND HERRING STOCKS

Barkley Sound (Fig. 1) is one of the major herring rearing grounds on the British Columbia coast. The sound is about 12 miles square and lies in a south-west-northeast direction between $48^{\circ} 47'$ and $49^{\circ} 02'$ North Latitude and between $124^{\circ} 35'$ and $125^{\circ} 35'$ West Longitude. The Barkley Sound herring stocks form the major portion of the herring population on the lower west coast of Vancouver Island subdistrict. This population is one of the ten major migratory populations making up about 95% of the total British Columbia stock (Taylor, Hourston and Outram, 1956). These populations were established on the basis of average differences in meristic characters and on the returns of tagged fish (Thompson, 1917; Tester, 1937, 1949; McHugh, 1954; Stevenson, 1955c). Intermixture between these major populations amounts to about 25% on the average, and is greatest between contiguous populations.

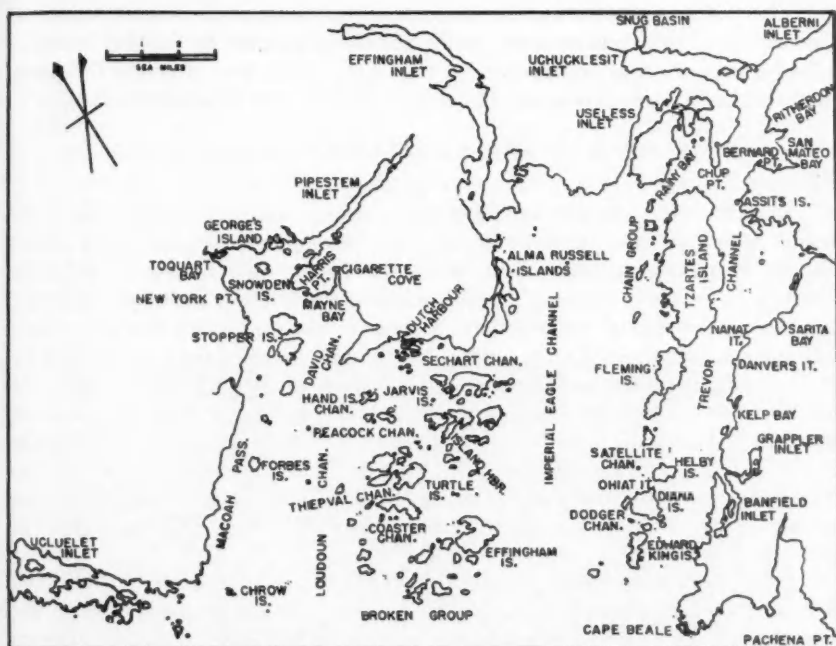


FIGURE 1. Map of Barkley Sound showing the major localities mentioned in the text.

The lower west coast population spawns in coastal waters between Pachena Point and Esteban Point. The summer feeding grounds are considered to be located off the outer entrance of the Strait of Juan de Fuca, and to extend southward off the northern coast of Washington (Stevenson, 1955c). Tagging studies (Stevenson, 1955c) have shown that about 83% of the herring that survive until the following year return to the inshore waters in which they spawned previously. Of the remainder, about 11% join runs of the population on the upper west coast of Vancouver Island (a population of comparable size whose summer feeding grounds are considered to be located off Nootka Sound and Esperanza Inlet) and 6% join runs of the population on the lower east coast of Vancouver Island (a larger population which migrates through the Strait of Juan de Fuca to feeding grounds off the northern coast of Washington).

APPROACH TO THE PROBLEM

The practical objective of this study was to obtain estimates of relative population size in the juvenile stage which might foreshadow fluctuations in year-class strength in the adult stage. However, before the size of a population can be reliably estimated, the extent of its distribution and the unit to which estimation procedures can be applied must be determined. To this end, a study of these aspects of the population dynamics of the juvenile herring was launched in Barkley Sound in 1951.

The problem of relating this information on the juvenile herring stocks to that on the adult populations was tackled at the same time by tagging juveniles with body cavity tags and recovering tags from the fishery after the fish were recruited to the spawning populations. These results will be reported later.

DISTRIBUTION OF JUVENILE HERRING IN BARKLEY SOUND

METHODS

SCOUTING. The simplest and most direct approach to determining the distribution is to look for or attempt to catch fish throughout the area under study. During the summer months schools of juvenile herring may be seen in the early morning and evening "flipping" at the surface in many of the sheltered inlets and bays in Barkley Sound. An experienced observer can distinguish the young herring schools from those of other species by the appearance of the rings formed by fins breaking the water surface and by the swimming motion and body shape of the fish. Juvenile herring "flips" generally show in groups of 6 to 20 in a small circle 1 to 3 feet in diameter. The rings formed by finning are distinct and usually have a single or double rim; the initial ring is about 2 inches in diameter. The school as a whole is usually 2 to 3 feet below the surface at dawn and dusk. The young herring swim with a smooth, graceful motion; their backs are green to purple in colour.

Other species present as schools of small fish may be distinguished as follows. Salmon (*Oncorhynchus* spp.) tend to flip singly and often jump right out of the water. Their backs are usually a lighter green in colour and the schools tend to stay more than 3 feet below the surface. Sand lance (*Ammodytes tobianus personatus*) swim with a distinctive undulating motion, generally just below the surface of the water. They break surface less often and the type of ring formed is more irregular and variable. Sticklebacks (*Gasterosteus aculeatus*) and sea-perch (*Cymotogaster aggregatus*) are usually smaller in size and swim just below the surface with a more leisurely motion. They produce very small, weak rings when they break surface. Anchovies (*Engraulis mordax*) are readily identified by a characteristic flashing of their gill covers.

DIP-NETTING WITH LIGHT. Various methods of capturing samples of fish were employed to identify fish located and to locate fish where none were observed. In 1951, samples of herring in the early juvenile stage were captured by a dip-net from schools attracted to a light at night. A 200-watt light backed by a reflector and hung just over the surface of the water proved more effective than less powerful or more powerful lights, and more effective also than submerged lights. The effectiveness of this method decreased rapidly as the fish grew and by mid-June, when the juveniles were close to 2 inches (5 cm.) in size, it had to be discarded. By this time, however, samples could be readily obtained by seining. Subsequent surveys were therefore concentrated in this period of greater accessibility of the juveniles.

HERRING RAKE. When the schools of juveniles were concentrated 6 inches to 3 feet (15-100 cm.) below the surface, samples of a few fish were obtained by use

of a herring rake. This is a long flat pole about 10 feet \times 2 inches \times $\frac{1}{2}$ inch (3 m. \times 5 cm. \times 12 mm.) with a comb-like projection of sharp 2-inch pins set along the long axis of the pole at half-inch intervals for about 3 feet from the end. The rake is passed quickly through a school of fish, prongs first, with a motion similar to that employed in paddling a canoe (Fig. 2). The direction of motion through the water is perpendicular to the direction of motion of the school so that the prongs will have an opportunity to impale some fish through the side. Up to about 20 fish may be caught per stroke, but in most cases the catch is 1 to 6 fish. This instrument is commonly employed by sport fishermen to obtain fresh bait, and stems directly from aboriginal models. Samples were raked in all years, mainly for the purpose of identifying schools.

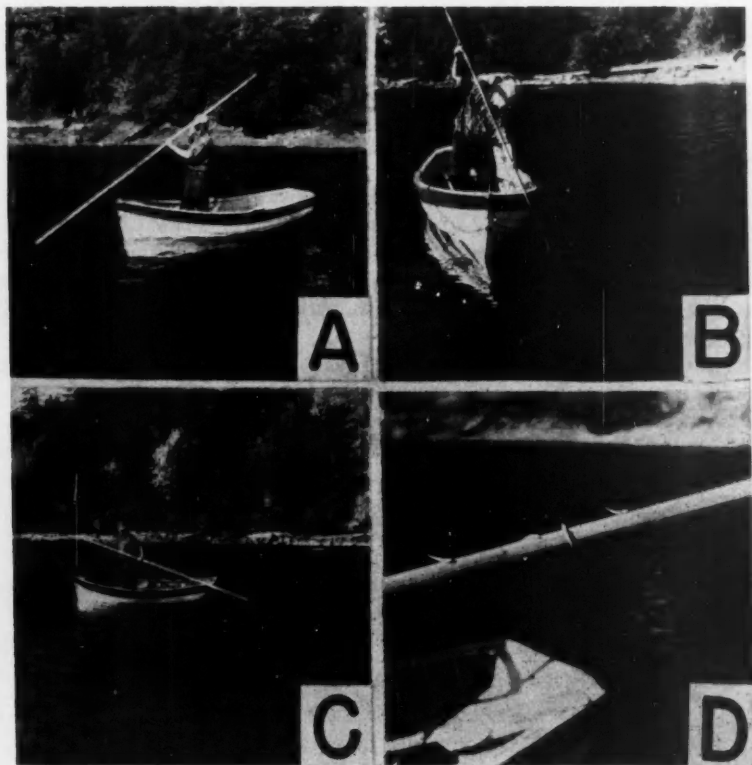


FIGURE 2. Raking juvenile herring.

- A. Rake poised for action.
- B. Rake in midst of stroke through a school of juvenile herring.
- C. Rake emerging from water with juveniles on prongs.
- D. Juveniles impaled on prongs.

SEINING. The most successful method of capturing juvenile herring was seining. Various mesh sizes, web preservatives and seine designs and sizes were tried throughout the 4-year period. Most of the seining was carried out with two types of net. The first was a drag seine of $\frac{3}{4}$ -inch cutched web 20 by 3 fathoms (36.5×5.5 m.), "hung in" 25%. Sets of 2,000–3,000 fish were readily made in the shallow waters (less than 5 fathoms) inhabited by the juveniles in early summer. In 1953 purse rings were attached to this net and it fished even more effectively. However, toward the end of the summer, as the juveniles grew larger and became more effective swimmers, they were found in deeper waters and tended to sound before this net could be closed. The second net, a 2-strip purse seine of similar web 37 by 6 fathoms (68×11 m.), was then employed. It proved effective on the larger fish in deeper waters and provided larger catches (up to 30,000 fish), which were more satisfactory for the marking and tagging programs.

Attempts to capture fish by other methods, including fyke net and miniature trawl, were unsuccessful.

In 1951, localities where appreciable numbers of juvenile herring were reported (Banfield Inlet, Uchucklesit Inlet and Pipestem Inlet—Fig. 1) were scouted visually throughout the day. When weather conditions were favourable, schools were almost always observed for 2 or 3 hours following dawn, and from about an hour before sunset to 1 to 2 hours afterward. Schools were occasionally observed during the day, mainly around docks and in well-shaded inlets, especially during the early part of the summer (the last week in June and the first two weeks in July). However, these daytime showings were sporadic and small compared to those at dawn and dusk. Scouting during the actual surveys was therefore confined to dawn and dusk.

Even when weather conditions were good for observation, schools sometimes failed to show where they were observed a few hours previously or afterwards. When weather conditions were poor they seldom showed at the surface at all. In partial compensation, scouting was also carried out with an echo-sounder during the 1952 and subsequent surveys. Schools were often observed at the surface at the same time, making the identification of the marks on the sounder as juvenile schools highly probable. Such schools usually made small shallow marks on the sounder paper (Fig. 3). Larger and deeper marks were observed where the fish were most abundant and at greater depths. Sets made on typical sounder marks usually yielded juveniles. Since young herring appear to make up the bulk of the small fish in this area, any marks that looked like juvenile herring and which could not be identified as arising from other sources were recorded as herring.

RESULTS

Juvenile schools were found mainly in inlets and bays, and in the back-edges behind islands and points, and in channels (Fig. 4). In these localities the water was usually relatively shallow (less than 100 feet deep) and currents were relatively weak but definitely present. The 1951 and 1952 observations were based on visual scouting only. In 1953 and 1954 echo-sounder observations were also

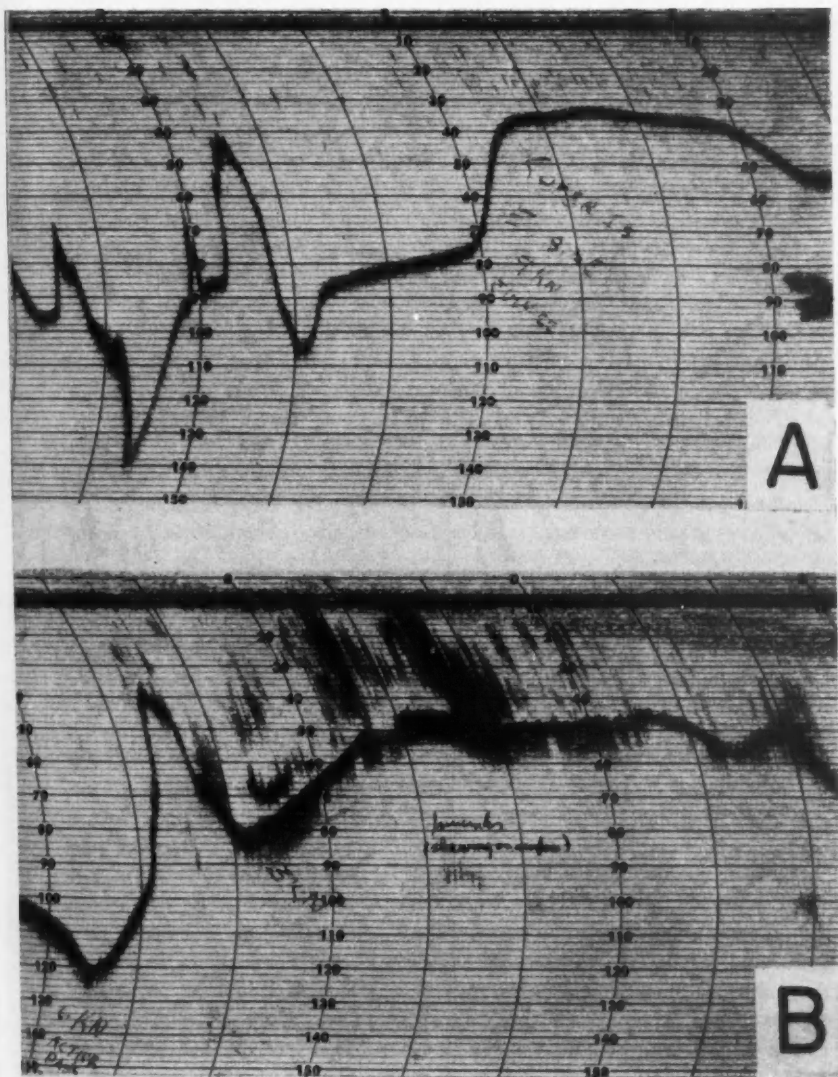


FIGURE 3. Echo-sounder tracings showing schools of juvenile herring.
A—Standard type marks; B—Very dense schooling.

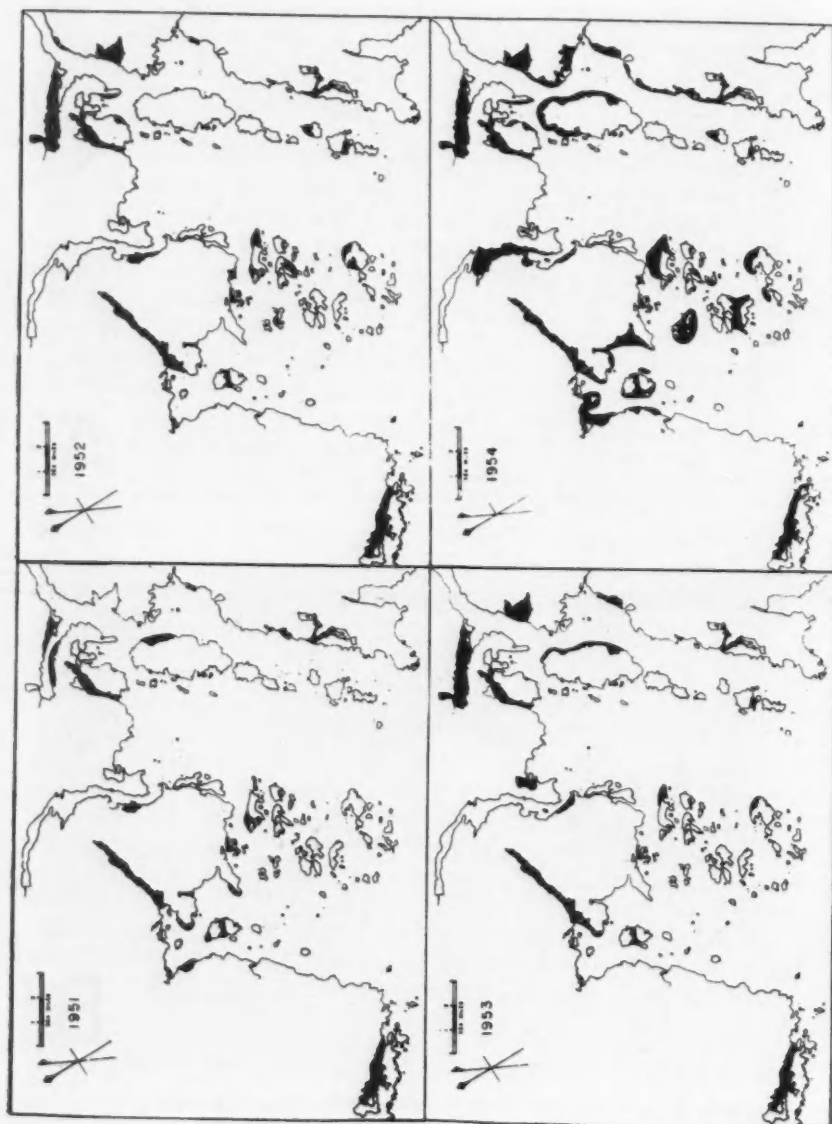


FIGURE 4. Localities in Barkley Sound where juvenile herring were found.

employed. Scouting in 1951 was of a preliminary nature and only localities in which juveniles had been reported, or which appeared to be good rearing grounds, were visited. Scouting was extended to cover some other localities in 1952 and 1953, but commitments to other aspects of the program precluded complete coverage. Not until 1954 was the whole sound thoroughly scouted; each locality was visited several times that year. The more extensive showing of fish in 1954 resulted more from finding stocks missed previously than from the presence of new stocks.

Both visual and sounder showings in thickly populated localities dropped off abruptly on leaving sheltered bays and back-eddies, and upon entering isolated spots in these localities where the wind had sufficient force to appreciably ruffle the surface.

Extensive scoutings of the large open channels failed to show any juveniles. Conditions for visual observation were generally poor, but even when conditions were good, few schools were observed. The echo-sounder tracings showed correspondingly few schools under all conditions. All coast lines were thoroughly scouted but fish were found consistently only in the more sheltered localities.

COMPOSITION OF THE BARKLEY SOUND JUVENILE HERRING POPULATION

One of the fundamental considerations in the population dynamics of the juvenile herring in Barkley Sound is the extent to which the juveniles form relatively discrete local populations or stocks within the sound or, conversely, the extent to which these stocks mix with one another. In the section on distribution it was shown that some groups of fish appear to be more or less isolated from each other geographically, which suggests the possibility of the existence of local populations or stocks within the sound. Two methods were used to investigate this possibility: (1) the recovery of marked fish, and (2) the analysis of the various stocks for differences in length composition.

MARKING PROGRAM

Fish from several of the larger concentrations in the sound were marked by the removal of different combinations of the paired fins. Fish captured by seining were transferred into a live pound at the site of capture by attaching the lead line of the seine to the rim of the live pound and "drying up" the net into the pound. Fish handled in this manner showed less injury than those transferred into the pound by dip-net. Every effort was made to avoid towing the pounds as this usually resulted in the removal of a considerable number of scales. Experiments on adults have shown that previous scaling increases tagging mortality tremendously. However, it was occasionally necessary to move the fish to a more sheltered spot. This was generally accomplished with little apparent damage by towing the pound very slowly (about one knot).

The pounds were rectangular enclosures of half-inch web. Tarred web was used (although it damaged fish scraping against it), as it was the only type of preservative that withstood the prolonged submergence these pounds were subjected to. A frame of 4×4 -inch lumber, 3×4 feet in size, floated on the

surface. The web was attached to this frame and fell down 5 feet to a bottom of similar meshed web attached to a 3×4 -foot frame of half-inch metal pipe. Thus the pound was collapsible for easy storage. Ropes attached to the four corners of the metal frame and drawn up through the corners of the wooden frame enabled the gradual drying up of the pound to reduce the size of the enclosure as the number of fish became less.

During the marking operations (Fig. 5), groups of about 100 fish were transferred by dip-net into a tray of half-inch Cuprinol web joining two "sticks" of 1-inch square lumber just over 4 feet long. These were set just inside one side of the pound and rested on the 4×4 's forming either end of the pound's frame. By rolling the web onto either stick the desired depth of the tray could be obtained.



FIGURE 5. Marking juvenile herring.

A. Markers, pound and tray.

B. Marking a fish by clipping off the left pelvic fin.

The side of the pound with the tray along it was lashed to the side of a row-boat. The markers sat in the boat facing lengthwise to the pound so that the tray was on their left side. A quick scoop of the left hand into the tray captured a fish in the palm of the hand. The fish was grasped belly up with the head pointing toward the marker's body and was held steady by the thumb on one side and the fingers on the other. In this manner all paired fins could be checked at a glance for previous marks without moving the fish, and the prescribed fins could be clipped off (Fig. 5b). The fish was then released immediately. In this manner up to 500 fish could be marked per hour by a skilled marker, and each fish remained out of water for less than 5 seconds. Mortality under these conditions proved relatively small (Appendix 1).

The most vulnerable period from the point of view of predation was immediately after release. The fish shot wildly off in any direction for the first few seconds, and then appeared to settle down to normal swimming behaviour and sought the nearest school. Predators, principally rockfishes (*Sebastes* sp.) and

sea-perches (Embiotocidae) congregated while marked fish were being released. However, concentrated hand-line fishing simultaneous with the marking seemed to remove the worst of this threat. Since the fish swam close to the surface until they regained their normal behaviour, any predation that occurred during this period was readily observed. On one occasion, in an effort to protect the freshly-marked fish from predation, some were released into a live pound. However, most of these fish injured themselves by dashing into the web sides of the pound during the initial shock, and this procedure had to be abandoned.

Experiments were carried out to determine the mortality caused by the marking operation. These indicated a mortality of from 1% to 16% (Appendix 1). It seems improbable that marking mortality under natural conditions exceeded 15%; and where experienced markers worked with fish that were in good condition, it appears to have been virtually negligible. Consequently no correction factor was applied to the numbers of fish marked.

Individual markings and recoveries (Tables I-IV) were summarized by locality for each year (Tables V-VIII for 1951 to 1954 respectively) and for the entire 4-year period (Table IX). With a few exceptions, more than two-thirds of the recoveries from each marking were in the locality of marking (Fig. 6). The exceptions are of three types:

(1) Groups of fish that disappeared from the locality during the summer after a strong early showing (Toquart Bay, 1951; Sechart Channel and Island Harbour, 1952).

(2) A population which showed a high degree of dispersion but continued to exist locally (Uchucklesit Inlet, 1952, 1954). This may have been a single stock behaving somewhat abnormally, or these fish, with others nearby, may have formed part of a larger stock.

(3) Two localities marked separately that appeared to contain the same population (Banfield Inlet and Kelp Bay, 1954).

TABLE I. Markings and recoveries of juvenile herring in Barkley Sound during 1951.

Marked at	Date	Number marked	Marked fish at		Recoveries from					
			Locality	Sound	Banfield Inlet	Cigarette Cove	Pipestem Inlet	Toquart Bay	Useless Inlet	All
Toquart Bay	July 18	946
Banfield Inlet	July 25	6,000
Cigarette Cove	July 30	1,000
Banfield Inlet	Aug. 2	273	6,000	7,946
Toquart Bay	Aug. 7	1,011	946	8,219
Cigarette Cove	Aug. 8	1,926	1,000	9,230	7	4	...	7	...	18
Useless Inlet	Aug. 15	2,348	...	11,156
Banfield Inlet	Aug. 20	8,650	6,273	13,504	7	1	...	1	...	9
Pipestem Inlet	Aug. 23	687	...	22,154
Useless Inlet	Aug. 25	2,185	2,348	22,841	1	...	1
Banfield Inlet	Aug. 27	1,430	14,923	25,026
Uchucklesit Inlet	Sep. 5	(3,188)	...	26,456	2	...	2
Banfield Inlet	Sep. 10	1,110	16,353	26,456	10	1	...	2	...	13
Useless Inlet	Sep. 12	5,000	4,533	27,566	1	5	6
Useless Inlet	Sep. 13	560	9,533	32,566
Useless Inlet	Sep. 14	860	10,093	33,126
Uchucklesit Inlet	Sep. 22	(1,607)	...	33,986
Uchucklesit Inlet	Sep. 26	(1,014)	...	33,986	2	2
Tzartes Island	Oct. 3	(4,164)	5	...	5
All localities		33,986 (9,973)			26	6	...	21	5	58

TABLE II. Markings and recoveries of juvenile herring in Barkley Sound during 1952.

Marked at	Date	Number marked	Marked fish at large		Recoveries from							All
			Locality	Sound	Banfield Inlet	Effingham Island	San Mateo Bay	Sechart Channel	Uchucklesit Inlet	Ucluelet Inlet		
San Mateo Bay	July 9	1,350
Uchucklesit In.	July 10	1,940	...	1,350
Effingham Is.	July 12	2,600	...	3,290
Sechart Channel	July 13	3,982	...	5,890
Island Harbour	July 14	3,140	...	9,872	1	1
Ucluelet Inlet	July 15	1,667	...	13,012
Banfield Inlet	July 19	1,320	...	14,679
Banfield Inlet	July 20	4,490	...	15,999
Ucluelet Inlet	July 29	2,590	1,667	20,489	3	1	...	4
Uchucklesit In.	Aug. 6	4,979	1,940	23,079
Banfield Inlet	Aug. 7	1,420	5,810	28,058
Banfield Inlet	Aug. 8	4,107	5,810	29,478
Ucluelet Inlet	Aug. 10	2,615	4,257	33,585
Banfield Inlet	Aug. 11	2,230	11,337	36,200	2	1	2	5
San Mateo Bay	Aug. 13	6,654	1,350	38,430	1	1
Uchucklesit In.	Aug. 15	7,027	6,919	45,084	1	1
Banfield Inlet	Aug. 17	7,121	13,567	52,111	1	2	3
San Mateo Bay	Aug. 18	3,336	8,004	59,232	6	...	1	7
Ucluelet Inlet	Aug. 21	1,980	6,872	62,568
Banfield Inlet	Aug. 26	818	20,688	64,548
San Mateo Bay	Aug. 27	9,544	11,340	65,366	2	1	3
San Mateo Bay	Sep. 23	2,033	20,884	74,910
Effingham Is.	Sep. 25	2,056	2,600	76,943
Ucluelet Inlet	Sep. 27	2,017	8,852	78,999
Ecoole Cannery	Oct. 1	2,064	...	81,016
All localities		83,080			3	0	11	5	5	3		27

TABLE III. Markings and recoveries of juvenile herring in Barkley Sound during 1953. Numbers bracketed under "Number marked" were checked only.

Marked at	Date	Number marked	Marked fish at large		Recoveries from							All
			Locality	Sound	Banfield Inlet	Pipestem Inlet	San Mateo Bay	Sarita Bay	Uchucklesit Inlet	Ucluelet Inlet	Vernon Bay	
Banfield In.	July 10	5,250
Uchucklesit Inlet	July 12	4,690	...	5,250
Uchucklesit Inlet	July 12	530	...	9,940
Banfield In.	July 16	7,030	5,250	10,470	2	2
Ucluelet In.	July 19	950	...	17,500
San Mateo B	July 20	2,010	...	18,450	1	1
San Mateo B	July 21	4,510	2,010	20,460
Banfield In.	July 23	10,400	12,280	24,870	7	7
Banfield In.	July 24	4,100	22,680	35,370	1	...	2	1
Banfield In.	July 25	1,730	26,780	39,470	1	...	1	...	2	6
Banfield In.	July 27	3,340	28,510	41,200	3
San Mateo B	July 28	5,340	6,520	44,540	1	1
Banfield In.	July 31	10,020	31,850	49,880	3	8
San Mateo B	Aug. 2	8,470	11,860	59,900	2	...	3	...	3	3
San Mateo B	Aug. 2	5,780	20,330	68,370	1	...	2	3
Useless In.	Aug. 4	5,030	...	74,150	1	1	2
Sarita Bay	Aug. 4	2,630	...	79,180
Uchucklesit Inlet	Aug. 6	5,000	5,220	81,810	2	2
Vernon Bay	Aug. 8	6,020	...	86,810
Pipestem In.	Aug. 9	5,700	...	92,830
Stopper Is.	Aug. 10	1,070	...	98,530
Banfield In.	Aug. 11	4,141	41,870	99,600	7	1	8
San Mateo B	Aug. 11	4,431	26,110	103,741	1	1
Sarita Bay	Aug. 13	4,298	2,630	108,172	3	1	1	5
Ucluelet In.	Aug. 13	1,850	950	112,470	1	...	1
Vernon Bay	Aug. 14	3,030	6,020	114,320	2	2
Uchucklesit Inlet	Aug. 15	4,240	10,220	117,350
Pipestem In.	Aug. 17	4,500	5,700	121,590	...	1	1
Banfield In.	Aug. 18	4,150	46,011	126,090	2
San Mateo B	Aug. 19	2,626 (7,020)	30,541	130,240	1	...	1	2
Sarita Bay	Aug. 21	3,629 (6,440)	6,928	132,866
Uchucklesit Inlet	Aug. 22	1,538 (5,180)	14,460	136,495	1	1
Pipestem In.	Aug. 23	3,155 (5,580)	10,200	138,033	1	1
Pipestem In.	Aug. 24	3,093 (4,320)	13,555	141,188
All localities		144,281 (28,540)			36	1	10	1	12	1	2	63

TABLE IV. Markings and recoveries of juvenile herring in Barkley Sound during 1954. Numbers bracketed under "Number marked" were checked only.

Marked at	Date	Number marked	Marked fish at large		Recoveries from							All
			Locality	Sound	Banfield Inlet	Kelp Bay	Pipestem Inlet	San Mateo Bay	Uchucklesit Inlet	Uchuelet Inlet	Useless Inlet	
Banfield In.	Jul. 21	5,510		
Banfield In.	Jul. 22	4,970	5,510	5,510	2	2
Uchuelet In.	Jul. 24	7,240	...	10,480
Uchuelet In.	Jul. 25	2,980	7,240	17,720
Uchucklesit Inlet	Jul. 27	10,070	...	20,700
San Mateo B	Jul. 28	10,110	...	30,770
Pipestem In.	Jul. 30	6,910	...	40,880
Banfield In.	Jul. 31	6,230	10,480	47,790	3	3
San Mateo B	Aug. 3	8,130	10,110	54,020	3	3
Uchucklesit Inlet	Aug. 5	4,620	10,070	62,150	4	4
Pipestem In.	Aug. 6	8,330	6,910	66,770	5	5
Uchuelet In.	Aug. 8	3,630	7,240	75,100	1	...	1
Banfield In.	Aug. 9	6,050	16,710	78,730	2	2
San Mateo B	Aug. 10	10,210	18,240	84,780	4	4
Uchucklesit Inlet	Aug. 18	8,190	14,690	94,990
Pipestem In.	Aug. 19	6,790	15,240	103,180	5	5
Uchuelet In.	Aug. 20	2,060	13,850	109,970
Banfield In.	Aug. 21	3,300	22,760	112,030
Banfield In.	Aug. 22	4,220	26,060	115,330
Uchucklesit Inlet	Aug. 25	6,210	22,880	119,550	1	1	1	3
Pipestem In.	Aug. 26	6,420	22,030	125,760	5	5
Uchuelet In.	Aug. 27	8,970	15,910	132,180	6	...	6
Uchuelet In.	Aug. 28	1,960	24,880	141,150
Banfield In.	Aug. 30	4,750	30,280	143,110	2	1	3
Kelp Bay	Sep. 1	6,190	...	147,680
Useless In.	Sep. 2	5,270	...	153,870
Kelp Bay	Sep. 3	4,210	6,190	159,140	...	3	3
Uchuelet In.	Sep. 3	(2,030)	26,840	163,350	2	2	2	...	6
Useless In.	Sep. 6	(6,050)	5,270	163,350	3	3
Kelp Bay	Sep. 7	(10,810)	10,400	163,350	2	1	3
All localities		163,350 (21,340)			14	4	15	9	7	9	3	61

TABLE V. Summary of markings and recoveries of juvenile herring in Barkley Sound in 1951.

Marked at	Number marked	Recoveries from					All
		Banfield Inlet	Cigarette Cove	Tzartas Island	Useless Inlet	Uchucklesit Inlet	
Banfield Inlet	17,463	17	7	2	26
Cigarette Cove	2,926	2	4	6
Pipestem Inlet	687
Toquart Bay	1,957	3	7	5	2	4	21
Useless Inlet	10,953	5	...	5
Totals	33,986	22	18	5	7	6	58

TABLE VI. Summary of markings and recoveries of juvenile herring in Barkley Sound in 1952.

Marked at	Number marked	Recoveries from					All
		Banfield Inlet	San Mateo Bay	Sechart Channel	Uchucklesit Inlet	Uchuelet Inlet	
Banfield Inlet	21,506	3	3
Brooke Cannery	2,064
Effingham Island	4,656
San Mateo Bay	22,917	...	8	3	11
Sechart Channel and Island Harbour	7,122	3	1	1	5
Uchucklesit Inlet	13,946	2	1	...	2	...	5
Uchuelet Inlet	10,869	3	3
Totals	83,080	8	10	1	2	6	27

TABLE VII. Summary of markings and recoveries of juvenile herring in Barkley Sound in 1953.

Marked at	Number marked	Recoveries from								All
		Banfield Inlet	Pipestem Inlet	San Mateo Bay	Sarita Bay	Uchucklesit Inlet	Ucluelet Inlet	Useless Inlet	Vernon Bay	
Banfield Inlet	50,161	26	1	5	3	1	...	36
Pipestem Inlet	16,448	...	1	1
San Mateo Bay	33,167	3	...	7	10
Sarita Bay	10,557	1	1
Stopper Islands	1,070
Uchucklesit Inlet	15,998	3	...	4	1	3	...	1	...	12
Ucluelet Inlet	2,800	1	1
Useless Inlet	5,030
Vernon Bay	9,050	2	2
Totals	144,281	32	2	16	5	3	1	2	2	63

TABLE VIII. Summary of markings and recoveries of juvenile herring in Barkley Sound in 1954.

Marked at	Number marked	Recoveries from							All
		Banfield Inlet	Kelp Bay	Pipestem Inlet	San Mateo Bay	Uchucklesit Inlet	Ucluelet Inlet	Useless Inlet	
Banfield Inlet	34,850	9	2	1	2	...	14
Kelp Bay	10,400	...	4	4
Pipestem Inlet	28,450	15	15
San Mateo Bay	28,450	1	7	1	9
Uchucklesit Inlet	29,090	5	2	...	7
Ucluelet Inlet	26,840	9	...	9
Useless Inlet	5,270	3	3
Totals	163,350	10	6	15	7	7	13	3	61

TABLE IX. Summary of markings and recoveries of juvenile herring in Barkley Sound over the period 1951-1954.

Marked at	Number marked	Recoveries from												All
		Banfield Inlet	Cigarette Cove	Kelp Bay	Pipestem Inlet	San Mateo Bay	Sarita Bay	Sechart Channel	Tzartas Island	Uchucklesit Inlet	Ucluelet Inlet	Useless Inlet	Vernon Bay	
Banfield Inlet	125,380	55	7	2	1	5	3	3	2	1	...	79
Cigarette Cove	2,926	2	4	6
Effingham Island	4,656
Kelp Bay	10,400	4	4
Pipestem Inlet	45,585	16	16
San Mateo Bay	84,534	4	22	1	3	30
Sarita Bay	10,557	1	5
Sechart Channel	7,122	3	1	...	1
Stopper Islands	1,070
Toquart Bay	1,957	3	7	5	4	...	2	...	21
Tzartas Island	4,164
Uchucklesit Inlet	64,843	5	5	1	10	2	1	...	24
Ucluelet Inlet	40,509	13	13
Useless Inlet	21,253	8	...	8
Vernon Bay	9,050	2	2
Totals	436,070	72	18	6	17	33	5	1	5	18	20	12	2	209

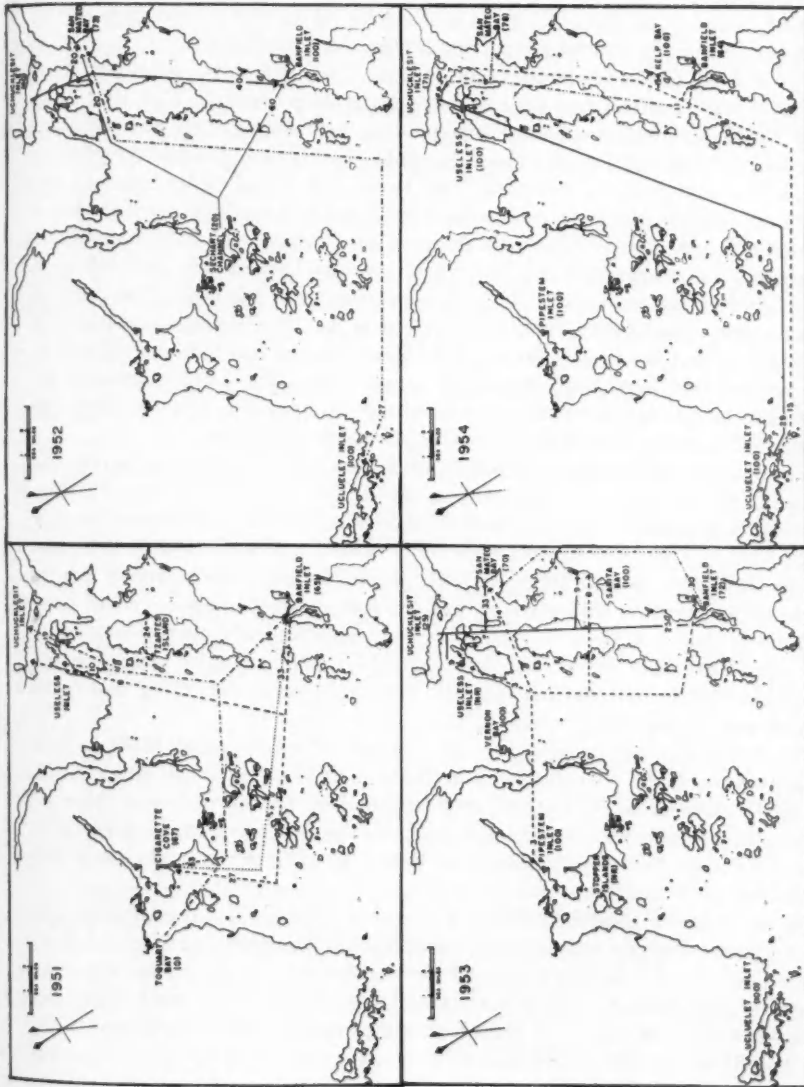


FIGURE 6. Migrations of the juvenile herring in Barkley Sound in 1951, 1952, 1953 and 1954 as indicated by the recoveries of marked fish. (Figures in parentheses by locality names indicate percentage of recoveries from markings made there which were taken in the locality of marking.)

The last-named situation is fairly well established since scoutings in 1954 showed that, at times, the schools of young herring extended along the entire one-mile coast between Banfield Inlet and Kelp Bay, and individual schools were observed from one of these localities to the other. Also, the composition of the two stocks is virtually identical (see length-frequency analysis).

The Uchucklesit Inlet picture is not as clear. This inlet is only two miles from San Mateo Bay, but the two are separated by a deep channel. The 1954 data (Table VIII) show no indications of extensive mixing between these two localities but in 1953 (Table VII) more Uchucklesit Inlet marks were taken in San Mateo Bay than in Uchucklesit Inlet itself. The movement seems to be more in the direction of San Mateo Bay than the reverse. If these two localities are considered to contain the same stock it too would fit the general pattern of less than one-third of the population emigrating. On the other hand the Uchucklesit Inlet fish may form a highly migratory stock which dispersed into the other localities in that general region, namely, into San Mateo Bay, Sarita Bay, Useless Inlet and Banfield Inlet. The fact that the San Mateo Bay fish, themselves, behaved like an individual stock favours this hypothesis. Mixing between these two localities would be expected to be greatest since they are closest geographically. The length-group analysis of the fish in these two regions favours this alternative.

A certain amount of mixing between the fish of Uchucklesit Inlet, San Mateo Bay and Banfield Inlet was apparent from the data from all years (Fig. 6). The 1953 data suggest that Sarita Bay and Useless Inlet fish also contributed to this mixing. Markings in Useless Inlet were also carried out in 1951 and 1954 but failed to show any mixing. However, only three markings were carried out in other localities after the 1954 marking, and the fish would scarcely have had time to migrate in that short period (1 to 5 days). In 1951 the only nearby locality in which markings were carried out was Banfield Inlet, and since only five recoveries were made from the Useless Inlet marking it is not surprising that none was made outside the inlet.

The 1952 recoveries suggest that the Sechart Channel-Island Harbour fish also participated in the general mixing in this region. Since these fish disappeared early in the summer and no appreciable numbers of fish were found there in other years, it is difficult to assess their role in the general picture unless it is assumed that these fish were transients on their way to form the stocks along the southeast side of the sound.

Considering the combined data for all years (Table IX), the fish in each locality (except the two transient groups in Sechart Channel and Toquart Bay, and the Uchucklesit Inlet fish discussed above) showed emigration by less than one-third of the stock. A limited amount of longer range cross-sound migration (i.e., movement across or around the sound to the opposite side) is indicated in all years. In 1951, seven (29%) of the Banfield Inlet recaptures were taken in Cigarette Cove, and movement in the reverse direction was 33% (7 marks); Toquart Bay marks were found in Cigarette Cove (33%) and in all localities studied on the southeast side of the sound (Banfield Inlet, 14%; Trevor Channel, 24%; Uchucklesit Inlet, 19%; and Useless Inlet, 10%). In 1952, three (27%) of the San Mateo Bay

marks were taken in Ucluelet Inlet. In 1953, one (3%) of the Banfield Inlet marks was recovered in Pipestem Inlet. In 1954, two (14.5%) of the Banfield Inlet, and two (29%) of the Uchucklesit Inlet marks were recovered in Ucluelet Inlet.

Over the 4-year period, emigration from the southeast to the northwest side of the sound amounted to 2.5% from Banfield Inlet to Pipestem Inlet; 2.5% from Banfield Inlet to Ucluelet Inlet; 10% from San Mateo Bay to Ucluelet Inlet; and 8% from Uchucklesit Inlet to Ucluelet Inlet. In the opposite direction, the emigration from Toquart Bay was 14% to Banfield Inlet, 24% to Trevor Channel, 19% to Uchucklesit Inlet and 10% to Useless Inlet. In addition, 33% of the Cigarette Cove fish emigrated to Banfield Inlet.

It would thus appear that there is some cross-sound migration, although the length-frequency analysis of the sampling data fails to indicate any extensive mixing. However, with the exception of the movement observed in 1951 eastward from the Toquart Bay-Cigarette Cove region to the southeast shore, these migrations appear to be less extensive than those between localities along either side of the sound. The 1951 migration may represent a late movement of juveniles into their natural rearing grounds as these fish disappeared from the Toquart Bay-Cigarette Cove region early in August and did not reappear. Thus, considering the results for the last three years only, the cross-sound migration is only about one-fifth that between localities on the same side of the sound (Table X).

TABLE X. Percentage movement of marked fish from one locality to other localities on the same side of the sound and from one side of the sound to the other. Actual numbers are given in parenthesis.

	1951	1952	1953	1954	1951-54	1952-54
Between localities	8	33	35	15	25	29
SE side	(2/24)	(7/21)	(21/60)	(5/33)	(35/138)	(33/114)
Between localities	64	..	0	0	19	0
NW side	(7/11)	..	(0/2)	(0/24)	(7/37)	(0/26)
SE side to NW side	23	13	12	11	10	7
of sound	(7/31)	(3/24)	(1/61)	(4/37)	(15/153)	(8/122)
NW side to SE side	59	0	0	0	29	0
of sound	(16/27)	(0/3)	(0/2)	(0/24)	(16/56)	(0/29)
Total movement on	26	33	34	9	24	24
one side of sound	(9/35)	(7/21)	(21/62)	(5/57)	(42/175)	(33/140)
Total movement	25	11	2	7	15	5
across sound	(23/58)	(3/27)	(1/63)	(4/61)	(31/209)	(8/151)

The extent of mixing between stocks bears a relationship to distance. Using the data for all four years, the number of recoveries taken at 5-mile intervals was as below. Distances measured followed shorelines and islands except where

Distance moved	Recoveries	
<i>miles</i>	<i>number</i>	<i>%</i>
0-1	137	66
1-5	28	12
5-10	17	8
10-15	14	7
15-20	11	5
20-25	5	2

major detours would have been involved. Thus the number of migrants decreases by about one-fifth each 5-mile interval from the area of tagging. These movements are, therefore, probably random. Fewer cross-sound migrations were observed because the distance is greater across the sound than between localities on one side. Indeed, no migrations were observed across the 10 miles separating the two major stocks on the northwest side (Pipestem Inlet and Ucluelet Inlet).

SAMPLING PROGRAM

Samples of over 100 of these fish were taken periodically from the major stocks located and preserved in 5% formalin. One hundred fish from each sample were later measured and weighed. The standard length of each fish (distance from the tip of the snout to the end of the fleshy part of the tail) was measured to the nearest half-millimeter, and each fish was weighed to the nearest twentieth of a gram. Sampling data were checked in three ways (Appendix 2). Randomness of selection of the fish preserved as a sample was checked by comparing two independent samples from the same catch. Average weights were checked by weighing the sample as a whole. (The average of these two determinations was taken as the sample average.) As a check on the randomness of selection of the fish sampled, the remainder of the fish preserved were weighed as a unit and their average weight calculated. Generally this average corresponded closely with that found for the sample. The number of samples taken in Barkley Sound in all years is given below along with the number of fish examined.

Year	1951	1952	1953	1954	All
Number of samples	56	65	91	76	288
Number of fish	3,700	8,276	12,306	9,667	33,949

Samples were also taken from other areas on the west coast of Vancouver Island (1952), the lower east coast of Vancouver Island (1951, 1952, 1953), from mortality experiments (1952, 1953) and from the fishery (1951, 1952). The total sampling for all years may be summarized as follows:

Year	1951	1952	1953	1954	All
Number of samples	116	90	192	76	474
Number of fish	8,247	16,834	15,621	9,667	44,369

LENGTH-FREQUENCY ANALYSES

Analysis of the sampling data indicated the presence of more than one size-group of juvenile herring in Barkley Sound, presumably reflecting the different ages of the various hatchings (Hourston, 1956). Since a frequency distribution from a single hatching usually forms a normal curve, frequency distributions of lengths of fish in samples from the various localities may be inspected for the presence of more than one normal distribution. This may be accomplished by direct inspection of the frequency plot for polymodal tendencies or by a graphic analysis of the various plots. Where the stocks in two localities are represented by

samples differing markedly in the number or size of the length groups, these stocks are not likely to have mixed to any great extent. Stocks that showed similar frequency distributions could have intermixed more freely (but need not have done so).

DIRECT ANALYSIS. Length-frequency distributions for the individual samples were plotted by locality in a time-scale series for each year (Fig. 7-10). When several samples were taken in the same locality over a short period of time, some plots overlapped each other and had to be displaced slightly in the time-scale to be distinguished. However, this displacement never exceeded two days.

In 1951 a particularly wide scatter was shown by the Banfield Inlet samples. At least four size-groups were prominent in the various samples and many more may have been present. At least two size-groups were apparent in the Cigarette Cove and Toquart Bay data. A single size-group dominated the other plots, but their wide size-range (e.g. in Pipestem Inlet) or skewed shape (e.g. in Trevor Channel) indicated the probable presence of other groups. It appeared from the size-range and the position of the major modes that the Banfield Inlet fish did not emigrate appreciably to other localities, although fish from the other localities could have joined the Banfield Inlet stock. However, the Cigarette Cove and Toquart Bay fish showed sufficiently similar distributions to admit of considerable mixing, as did the Uchucklesit Inlet, Useless Inlet and Trevor Channel fish. The latter group of fish appeared to be longer than the former. The single Pipestem Inlet sample was scarcely sufficient for adequate comparison but could have showed some mixing with the Cigarette Cove and Toquart Bay fish.

In 1952 considerable scatter and variability was again demonstrated by the Banfield Inlet samples; at least three modes were apparent. In the Broken-Group samples the distribution was similar to that in Banfield Inlet, but was less erratic, indicating that migration from the Broken-Group to Banfield Inlet was quite possible. The San Mateo Bay samples also showed a wide scatter and at least three modes, but these tended to be at a greater length than those for the Banfield Inlet fish. Migration from Uchucklesit Inlet to San Mateo Bay was compatible with the length-frequency distributions, but, due to the smaller range in size and the unimodal distribution of the former fish, migration in the opposite direction was less likely. The Ucluelet Inlet fish had a more or less unimodal distribution and tended to be much smaller than those in other localities. The single Useless Inlet sample resembled the Uchucklesit Inlet ones in distribution but was characterized by a larger size-range. The Cigarette Cove fish resembled the Ucluelet Inlet fish in their mode but exhibited a wider size-range. On this basis, neither the Banfield Inlet fish nor the San Mateo Bay fish joined other stocks in appreciable numbers although these two stocks may have intermixed. The Broken-Group fish could have joined the Banfield Inlet stocks or the Uchucklesit Inlet stocks in appreciable numbers early in the season. There may have been some emigration from Uchucklesit Inlet to San Mateo Bay. The Ucluelet Inlet fish appear to have remained more or less isolated.

In 1953 sampling was concentrated in a shorter time period and major trends were therefore more evident. Again the Banfield Inlet and San Mateo Bay plots showed considerable scatter and variability; each indicated a minimum of four size-groups. Mixing between these two groups was quite possible, although the main modes tended to be at greater lengths in San Mateo Bay. The Useless Inlet samples were also characterized by a considerable scatter, although one major mode was evident. This scatter could be accounted for by limited emigration from the Banfield Inlet or San Mateo Bay stocks, or from both. Ucluelet Inlet fish also varied considerably but from the last week in July were dominated by one size-group of relatively small fish. About the same time a dominant group of fish of similar size appeared in Pipestem Inlet; it also appeared in the Stopper Islands, although a larger size-group dominated one of these samples. The ubiquitous presence of this size-group in localities along the north-west side of the sound could indicate a general mixing in this area, or could indicate that these localities shared the results of the same spawnings more or less equally. In any event, this

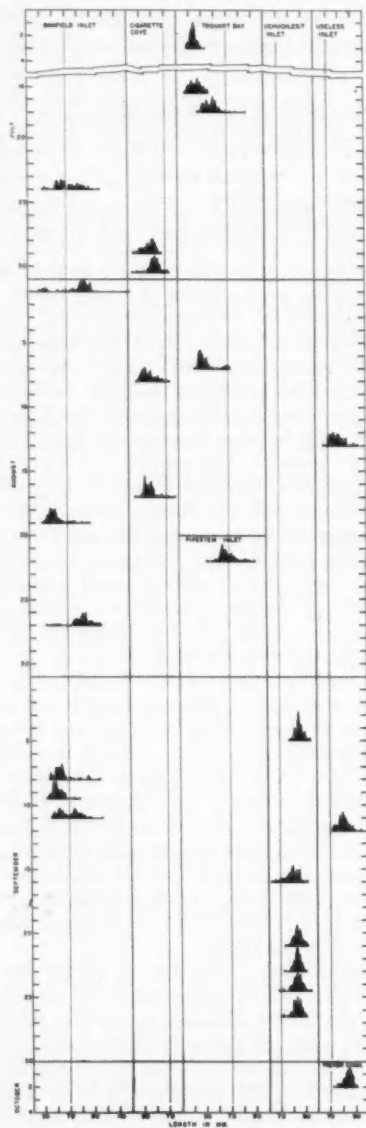


FIGURE 7. Frequency distributions of the standard lengths of juvenile herring in the 1951 samples plotted on a time scale according to date of capture.

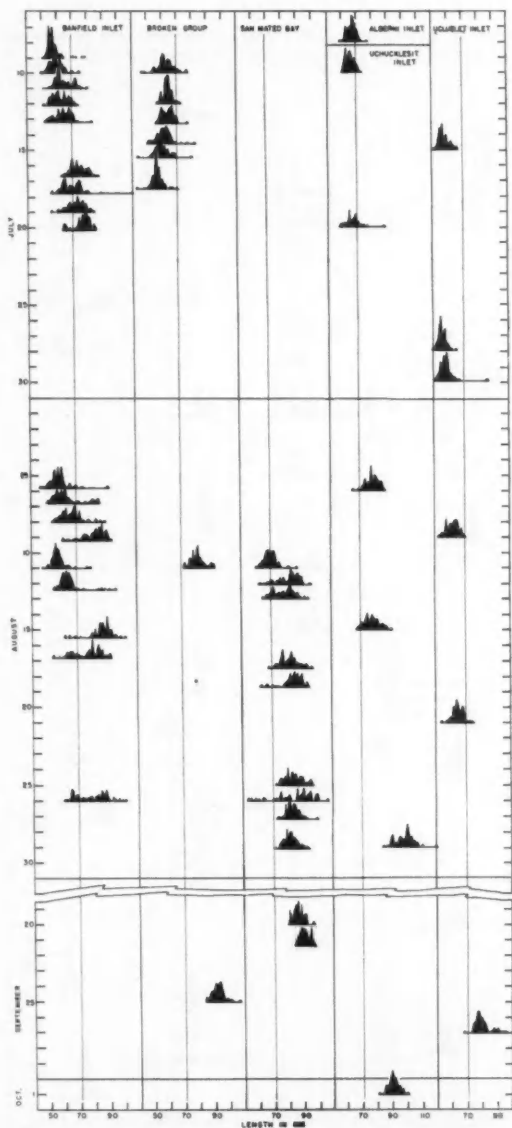


FIGURE 8. Frequency distributions of the standard lengths of juvenile herring in the 1952 samples plotted on a time scale according to date of capture.

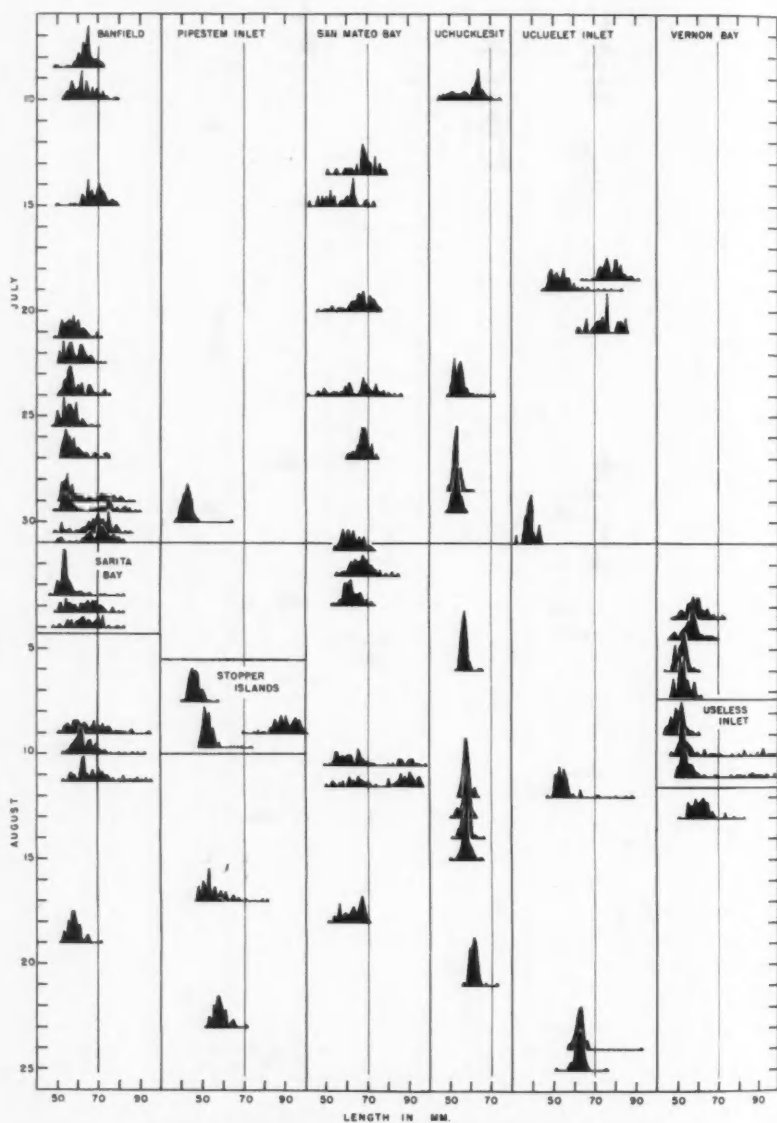


FIGURE 9. Frequency distributions of the standard lengths of juvenile herring in the 1953 samples plotted on a time scale according to date of capture.

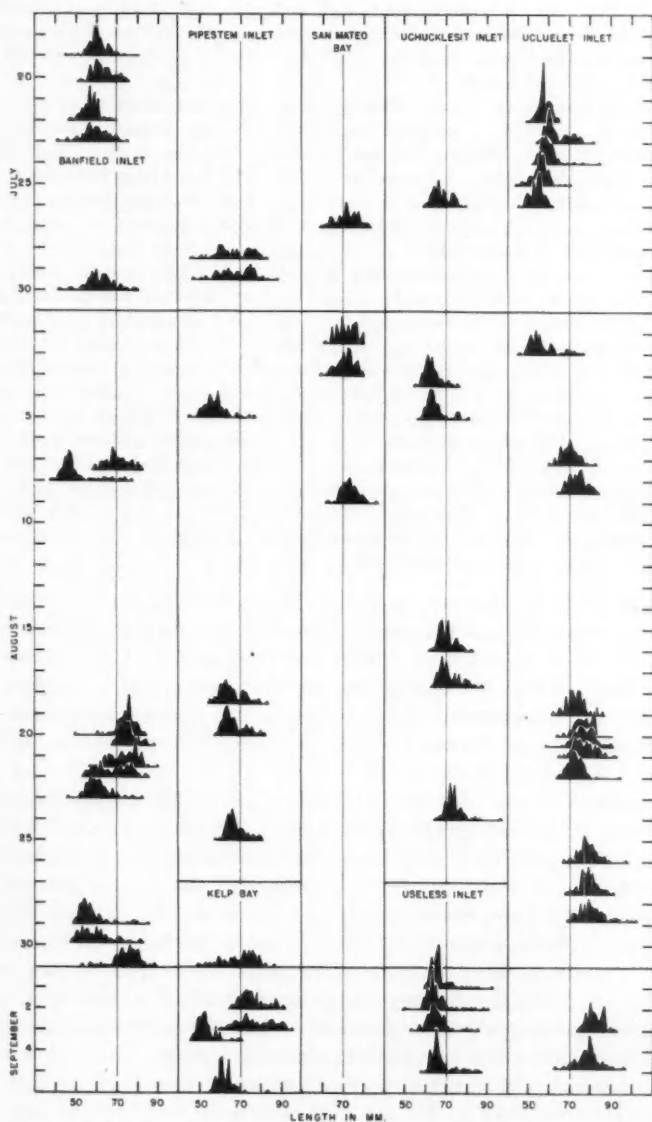


FIGURE 10. Frequency distributions of the standard lengths of juvenile herring in the 1954 samples plotted on a time scale according to date of capture.

size-group distinguished the stocks on that side of the sound and indicated that mixing was relatively limited with the stocks elsewhere. A slightly larger but slower-growing size-group markedly dominated the Uchucklesit Inlet stock and appears to have been present but less dominant in the Useless Inlet and Vernon Bay stocks. Mixing between these three localities was also quite possible, but the small size-range shown by the Uchucklesit Inlet fish indicates little immigration into this locality.

In 1954 the samples were again concentrated in a short time interval. A wide size-range and considerable variability were again demonstrated by the Banfield Inlet samples. This feature is shared with the Kelp Bay fish, and the fish in these two localities could have mixed freely. At least three size-groups were present in each. The San Mateo Bay samples failed to show the scatter and variability noted in other years. One size-group dominated throughout, although at least two others were probably present. These fish appeared to be larger than the dominant size-groups in Banfield Inlet. A single smaller size-group dominated in Uchucklesit Inlet although at least two others were present there. In Useless Inlet an even smaller size-group dominated; considerable scatter was evident, made up of at least three size-groups of larger fish. Thus, each of the stocks on the southeast side of the sound appeared to be characteristically different. The scatter evident in all may reflect limited immigration from the other stocks. Ucluelet Inlet and Pipestem Inlet fish also showed considerable scatter in their length-frequency plots, with one size-group dominating. In Pipestem Inlet this was the smaller size-group (which was roughly about the same size as the smaller dominant group in Banfield Inlet). In Ucluelet Inlet, a slightly larger size-group dominated, but at least one smaller and two larger size-groups were included. Limited mixing between these two localities was likely, as the dominant size-group in each was evident as a secondary size-group in the other. Some mixing between Ucluelet Inlet and San Mateo Bay and/or Uchucklesit Inlet was also possible on this basis.

In all years, the extensive scatter shown by the Banfield Inlet samples could reflect immigration from any and all other localities.

PROBABILITY PLOT ANALYSIS. A method of separating a frequency-distribution plot into its theoretical normal curve components by plotting probability graphs has been described by Harding (1949) and discussed by Cassie (1950, 1954). Since the length-frequency distribution for the progeny of a single spawning should form a normal curve, this procedure seemed promising as a method of sorting out size-groups of juveniles resulting from the contributions of different hatchings.

The procedure is to plot the cumulative percentage length-frequencies for the sample on probability graph paper. Single size-groups or normal curves are "probably" represented by a single unbroken line. Where the trend line shifts in slope or position, a new size-group is indicated, with the point of inflection of the sigmoid curve joining two succeeding lines representing the division between the two size-groups. Plots showing the presence of one, two, three and five size-groups (Fig. 11) illustrate the procedure. It was sometimes difficult to determine whether a series of points represented a new size-group or merely the sigmoid curve joining two other size-groups; when the number of fish involved was relatively large, the points were considered to represent a new size-group.

Each size-group determined in this manner is then replotted as a single frequency distribution (Fig. 11) with the ordinate (length) corresponding to 50% representing the mean of the group, and the range between 16.7% and 88.3% representing two standard deviations. The normal curves represented by these lines may then be plotted over a histogram of the observed frequencies to indicate the length-group composition of the sample (Fig. 11).

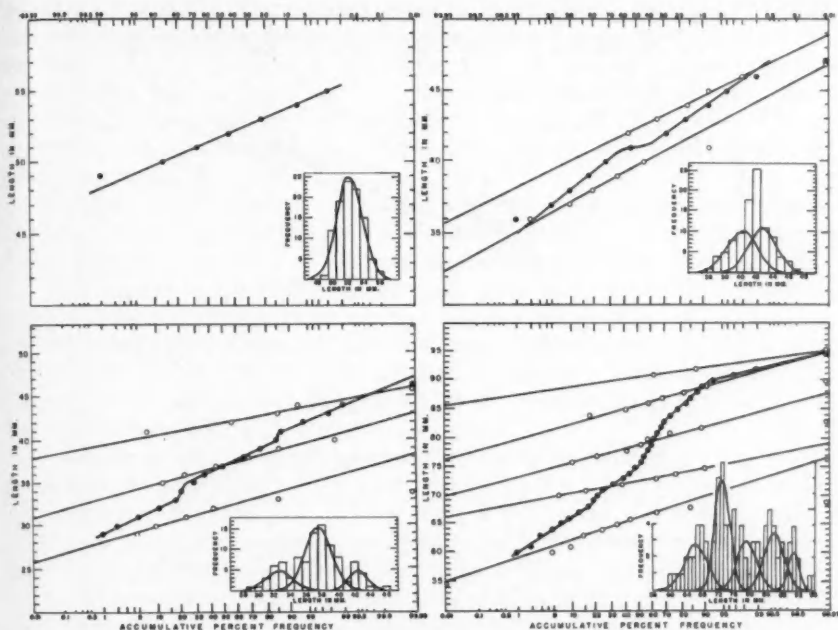


FIGURE 11. Probability plots of length-frequency distributions for a unimodal sample, a bimodal sample, a trimodal sample and a pentamodal sample.

There were a large number of spawnings (13 to 19) each year in Barkley Sound, and a certain amount of mixing throughout the sound was indicated by the marking studies. Detecting as large a number of size-groups as this in probability plots, and relating them to the various spawnings would be exceedingly difficult, if not impossible.

Therefore, as a test of the method, an analysis was run on the Departure Bay samples from 1950 to 1953 inclusive (Appendix 3). There were only three or four major spawnings per year in this region and it should be reasonably easy to detect that number of size-groups by this method. In each year the number of size-groups found corresponded with the number of major spawnings in the region. It would therefore appear that these size-groups were due to the age differential resulting from spawnings at different times, and thus that this graphic analysis probably detected real differences. Indeed, the size-group means determined in this manner for the Departure Bay data for 1950 and 1951 formed four and three relatively clear cut lines with very little scatter in a semi-logarithmic plot of length against date of capture (Fig. 12), whereas a similar plot of the sample means for 1950 and 1951 showed a considerable amount of scatter.

The method has a number of limitations, namely:

(1) Lines were fitted by sight to the probit plots. On some diagrams more than one set of lines could be interpreted. If the scatter of the points about the

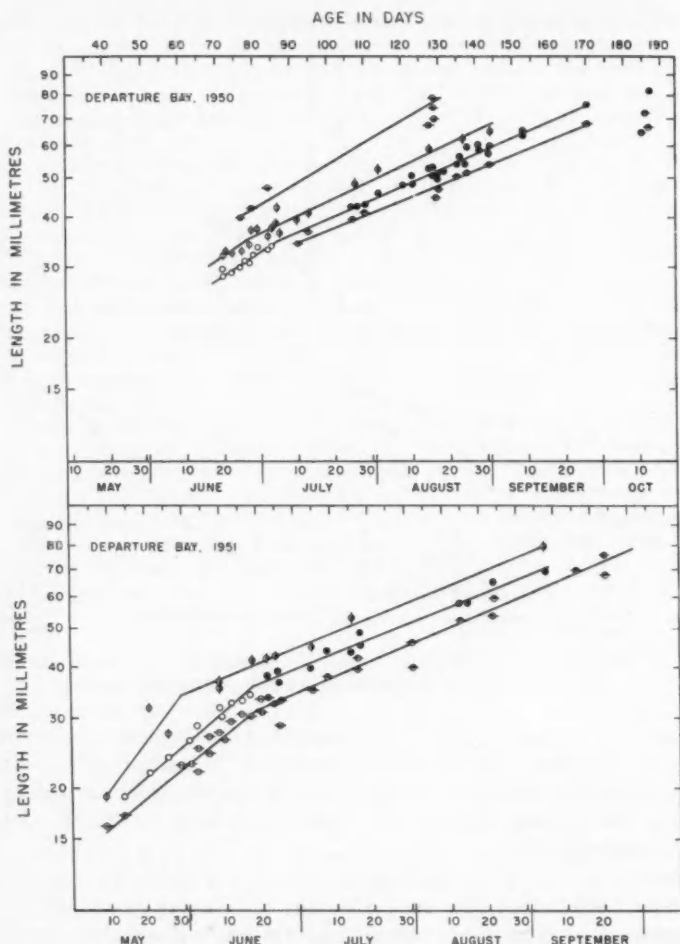


FIGURE 12. The relationship of the logarithm of length to date of capture, for different size-groups of juvenile herring in Departure Bay during 1950 and 1951.

proposed lines was relatively large, a questionable break was usually considered unreal but if the scatter was small, the questionable group was accepted.

(2) When a frequency distribution showed considerable variation in the "tails" of the curve, it was often impossible to sort out more than one group with any degree of confidence as the number of fish involved was usually very small.

(3) Since the size-range in some samples taken at approximately the same time differed widely, the maximum number of size-groups in any one sample

would not represent the maximum number in any locality. Consequently it was necessary to plot the size-group means and fit growth curves (straight lines on a semi-logarithmic plot) to the points to estimate the number of size-groups found in the locality. When a large number of points were involved, the number of lines represented was not clear. In such plots, the minimum probable number of lines were drawn. This was sufficient to indicate lack of mixing with stocks containing only a few size-groups.

(4) Individual size-groups may not be represented by normal curves in a frequency distribution. Predation could be rather specific to size, distorting the normal curve so that probit analysis would indicate more than one size-group.

Thus erroneous conclusions could easily have been drawn for individual samples. However, when a series of samples shows consistent trends, as for the juvenile samples from Departure Bay, it is highly probable that real differences are being detected. The fact that the number of size-groups found in the juvenile samples from Departure Bay corresponds with the number of major spawnings in that locality lends additional validity to the results.

The method was therefore applied to the Barkley Sound data. The means of the length-groups were plotted logarithmically against time for the six most heavily sampled localities (Fig. 13). Lines were fitted visually to these means in an effort to clarify the number of size-groups involved. In some diagrams other sets of lines could have been drawn but would not have affected materially the number of size-groups. While the maximum number of size-groups in any one sample was six, different samples were taken on the same or successive days indicated groups beyond the size-range of other samples and thus the presence of a larger number of groups in some localities. In all diagrams the number of size-groups indicated was greater than could clearly be observed in the direct analysis of the length-frequency plots.

Sampling was not sufficiently intensive in 1951 to permit much comparison between localities. In Banfield Inlet, the only locality where sampling was sufficiently intensive to permit an estimate of the number of size-groups, six size-groups were detected. Scanty sampling in Pipestem, Uchucklesit and Useless Inlets showed three size-groups in each. Thus appreciable immigration to the latter localities from Banfield Inlet appears unlikely as the smaller size-groups in Banfield Inlet were not detected elsewhere.

In 1952, nine size-groups were found in Banfield Inlet, precluding extensive emigration of these fish to other localities, all of which contained fewer size-groups. Six size-groups were found in San Mateo Bay, but they tended to be larger than those in Banfield Inlet, in mid-August at any rate. However, their apparently slower growth rate would eliminate this difference by mid-September. Thus some intermixture may have taken place between these two localities. Similar slopes to those found in Banfield Inlet were shown by the Uchucklesit Inlet size-groups but these fish were larger, more the size of the San Mateo Bay fish. Some of these fish could have joined the San Mateo Bay fish but the large number of size-groups in the latter locality precludes appreciable movement in the opposite direction. The four Useless Inlet size-groups were also found in Banfield Inlet so some of these fish could have moved to Banfield Inlet. The four size-groups found in Ucluelet Inlet were smaller than those found elsewhere, except for the smaller size-groups in Banfield Inlet. Since the latter had a greater slope, mixing either way could not have been extensive. These conclusions are all in agreement with those found in the direct analysis.

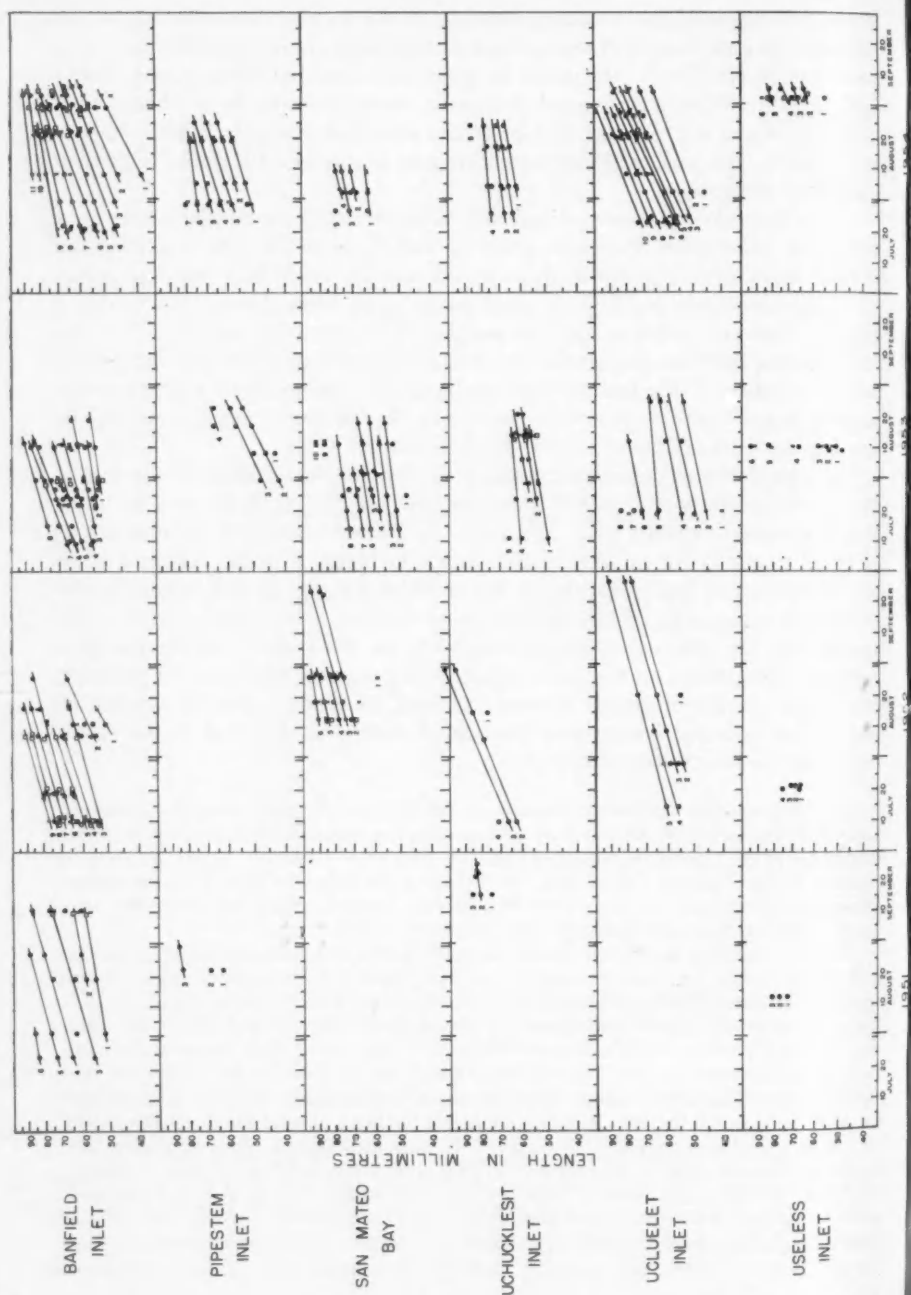


FIGURE 13. The relationship of the logarithm to length to date of capture, for size-groups within samples from six of the most extensively sampled localities in Barkley Sound.

In 1953, eight size-groups were found in the Banfield Inlet data. Ten were found in San Mateo Bay but these had smaller slopes. However, because of the complexity of both diagrams the slopes could have been interpreted differently in either case, and consequently these two stocks could have intermixed. The Uchucklesit Inlet plots showed slopes comparable to those found in the San Mateo Bay plots, and their five length-groups were all represented in San Mateo Bay (numbers 2, 3, 4, 6 and 7). Consequently, Uchucklesit Inlet fish could have migrated to San Mateo Bay in appreciable numbers, but movement in the opposite direction could not have been extensive. The Ucluelet Inlet samples had the widest size-range early in the season with eight size-groups appearing. The Pipestem Inlet fish were small; three of the four size-groups found corresponding roughly to numbers 1, 2 and 4 in Ucluelet Inlet. Thus there may have been some migration from Pipestem Inlet to Ucluelet Inlet but little movement in the opposite direction was likely. The smaller size-groups in these two localities were not found elsewhere, indicating very little emigration to localities on the other side of the sound. The six size-groups in Useless Inlet were again found in Banfield Inlet, indicating some Useless Inlet fish may have migrated to Banfield Inlet. This is in agreement with the results of direct analysis.

In 1954 the Banfield Inlet data again showed a large number of size-groups (eleven). Ten size-groups were found in Ucluelet Inlet, but these covered a smaller size-range and tended to be bigger fish. Their trend lines had greater slopes than those for Banfield Inlet. The Kelp Bay fish seemed to fit the pattern shown by the Banfield Inlet fish and were plotted on the same graph. The six size-groups found in Useless Inlet corresponded fairly closely with numbers 2, 5, 6, 7, 9 and 10 in the Banfield Inlet-Kelp Bay plot; Useless Inlet fish may therefore have migrated in appreciable numbers to Banfield Inlet, but migration in the opposite direction would have been limited. Both the San Mateo Bay and Uchucklesit Inlet plots were again characterized by smaller slopes. The five Uchucklesit Inlet groups corresponded roughly with the five groups in San Mateo Bay and the two groups of fish could have mixed freely. These size-groups could also have corresponded to the larger size-groups in Useless Inlet, although the difference in the time of sampling precludes accurate comparison. A relatively large number (seven) of size-groups was also found in Pipestem Inlet, representing a wide size-range. These size-groups did not correspond closely with those in any of the other localities.

The direct analysis of the length-frequency distributions indicated some mixing between San Mateo Bay, Uchucklesit Inlet and Useless Inlet but the dominance of different size-groups in these localities showed that this mixing was limited, not relatively free as indicated above. On the other hand, the former analysis shows some mixing between Pipestem Inlet and Ucluelet Inlet was likely, whereas the probability plot analysis shows this was unlikely. Mixing between Ucluelet Inlet and San Mateo Bay and Uchucklesit Inlet was also not very probable according to the latter analysis.

CONCLUSIONS ON COMPOSITION

On the whole, the results of the length-frequency analysis support the conclusions from the marking experiment. These include:

- (1) The Banfield Inlet and Kelp Bay fish form a single stock.
- (2) The Toquart Bay fish mix freely with those in Cigarette Cove, possibly forming a single stock.
- (3) Other localities appear to contain relatively discrete stocks.
- (4) These stocks mix to some extent.
- (5) The 1952 Sechart Channel and Broken Group fish that disappeared in mid-summer moved to the southeast side of the sound, mainly to Banfield Inlet.
- (6) The 1951 Toquart Bay-Cigarette Cove fish that disappeared early in the summer migrated to various localities on the southeast side of the sound.
- (7) The results of the marking program left the status of the Uchucklesit Inlet fish unsettled. However, the difference in composition of the Uchucklesit

Inlet and San Mateo Bay fish found every year except 1954, indicates that these two groups of fish did not form a single stock. Uchucklesit Inlet fish migrated to San Mateo Bay in 1952 and especially 1953 but only one San Mateo Bay mark was recovered in Uchucklesit Inlet, and that was in 1954 when the composition of these two stocks was more similar than in other years. The Uchucklesit Inlet fish may, therefore, be considered to have formed a single stock which showed stronger migratory tendencies than the other stocks studied.

Thus the Barkley Sound juvenile herring population during these years was made up of a series of individual stocks which mixed somewhat, but not enough to destroy their identity. These stocks contained varying numbers of size-groups, presumably the progeny of different spawnings, so that they differed somewhat in the average length of the fish and in growth-rates. Growth patterns varied from year to year and may have differed significantly from those observed in other major herring populations.

ABUNDANCE OF JUVENILE HERRING IN BARKLEY SOUND

A general estimate of the juvenile herring population in Barkley Sound was made each year from a scouting survey. More precise estimates of some of the major stocks were made by Schnabel-type marking experiments. These more precise estimates were then employed to provide a correction factor for the general estimate, which was invariably low, since all the fish in any locality were seldom observed in any scouting.

SCOUTING SURVEYS

Scouting for juvenile herring consisted mainly of visual observations of schools flipping at the surface. The juvenile schools were readily observed when they broke surface, usually in the early morning (dawn to sunrise) and late evening (sunset to dusk). They occasionally appeared during the day also, especially when they were abundant, but such appearances were not consistent. Many of these schools were seined to obtain fish for marking and thus enabled counts of the number of fish in these schools. The results were applied in estimating the number of fish seen in a locality. General estimates according to a scale of abundance were made at first but these were soon supplemented by absolute estimates of abundance. Since the extent to which the fish show at the surface varies with weather conditions, these conditions were also recorded at the time of observation. Observations made under poor weather conditions were repeated under good conditions in order to obtain more reliable estimates of distribution and abundance.

Early in the summer the schools tended to be relatively small, consisting of a few hundred fish. As time passed the schools grew larger and by mid-July most contained several thousand fish (averaging about 10,000). When these schools showed at the surface in calm water, several flips could be seen at one time, generally in a circle 1 or 2 feet in diameter. The surface area actually occupied by such schools appeared to be about 20 to 30 feet square (6-9 m.). In late summer and early fall (mid-August on) the schools often mingled to form large

masses of fish; sometimes over a million fish would be schooled together in this manner. Such bodies of fish were estimated in terms of the number of "normal" (10,000 fish) schools they contained from the number of "groups" of flips showing (several flips in a small circle) and by the area they occupied.

The problem of weather conditions during observation was alleviated somewhat in 1952 and succeeding years by the application of the echo-sounder to these surveys. When the fish were right at the surface, the echo-sounder would not pick them up, but below a depth of about ten feet (3 m.) they produced marks on the sounder paper. At a speed of 7 to 9 knots (13-17 km./hr.) many such marks appeared as tiny lines about 1.5 mm. deep (the distance between two fine lines on Bendix sounder paper), and one to three scratches wide (Fig. 3). Sets by purse-seine on some of these marks showed that the schools contained about 10,000 fish. Fish observed in this manner were included in the total estimates. Adult herring populations have been estimated by this means, although certain difficulties are intrinsic in the method (Hourston, 1953a,b). Sometimes it was difficult to identify marks as juveniles, but since juvenile herring made up the largest portion of the fish in this area at this time, marks were concluded to represent juveniles unless there was reason to believe otherwise (e.g. salmon, sand lance or adult herring observed in the vicinity).

From tables of the estimated numbers of juvenile herring seen during each observation, the maximum single estimates (i.e. the largest number of fish observed at one time in each locality) were summarized for each year (Table XI). With the exception of 1953, the estimates increased yearly. It is thought that the observed increase stems from more extensive and efficient scouting rather than a general increase in abundance of the juveniles. In 1953 efforts to make the scouting more critical in order to standardize procedures apparently resulted in a general underestimate of abundance. Also, since weather conditions were poorer in 1953 than in other years, a smaller portion of the fish may have been seen that year. The number of localities scouted was not increased over 1952. In any case the drop in the total number of fish observed in 1953 is not regarded as significant.

A more representative index of relative annual abundance may be obtained by comparing the abundance in localities which were scouted both years. On this basis 4 localities out of 12 showed an increase in 1952 over 1951, 8 showed a decrease, and 2 showed no change. In 1953 there was an increase in the estimates for 3 of the 11 localities over the 1951 estimates, a decrease in 10 localities, and no change in the remaining one. In 1954 more fish were observed in 10 localities than in 1951, whereas fewer fish were observed in 4 localities; no change was indicated in the other locality. In 5 out of 21 localities the stocks were larger in 1953 than in 1952; in 14 they were smaller, and there was no change in 2. In 1954 the number of fish seen was greater than in 1952 in 16 localities; it was less in 3 localities and there was no change in the 3 other localities. In 21 out of 23 localities the estimates were higher in 1954 than in 1953; in the other 2 localities a decrease was indicated. On this basis the 1954 year-class was much stronger than any of the others. The 1951 year-class was the next strongest, followed by 1952

and 1953. However, since the 1953 year-class is thought to have been underestimated, the order of abundance could read 1954, 1953, 1951 and 1952. In any event, the 1954 year-class appears to be relatively strong, the 1952 year-class relatively weak and the other two probably intermediate.

MARKING EXPERIMENTS

Schnabel-type marking experiments (Schnabel, 1938) were carried out on several of the larger stocks each year in order to estimate the number of juveniles present. A marking and recovery program of this type, where the recoveries are made while marking is in progress, lends itself well to the conditions of this study, since fishing mortality is relatively low, and the only opportunity to search for marked fish occurs in the experimental catches. Thus fish are examined for previous marks with each marking after the first. Fish were marked by the removal of various combinations of the paired fins.

Since the Barkley Sound population was made up of a series of local stocks, as determined above, a single experiment for the whole sound would not satisfy the assumption of a homogeneous population. However, as a method of estimating the size of the individual stocks this assumption was satisfied. Other prerequisites of this type of experiment (Ricker, 1948) were approximated by this study. The marked fish could not lose their mark over the period of the investigation, and were readily recognized. It is presumed that marked and unmarked fish were equally vulnerable to capture by seining. Some mortality of marked fish did occur but was comparatively small (Appendix 1) and, presumably, rather constant. Consequently, the mortality would not have affected comparative estimates, and would have affected absolute estimates only slightly. Some migration took place in and out of these localities but it would not have been sufficient to mask major differences in population size, although it could have affected somewhat the absolute value of the population estimate.

In population estimates of this nature, the number of marked fish recovered must be sufficiently large to provide reasonably small confidence limits for the population estimate. Also, the number of times recoveries are made should be sufficient to establish a "levelling off" of the estimate. In some tests these conditions were not satisfied, especially in the earlier years when techniques were being developed.

TABLE XI. The maximum single estimates of the number of juvenile herring in each locality surveyed during the study in thousands.

Locality	Thousands of juvenile herring			
	1951	1952	1953	1954
Alberni Inlet	..	203
Assits Island to Congreve Island	250
Banfield Inlet	1,000	1,150	200	600
Banfield Inlet to Kelp Bay	200
Bernard Point to Assits Island	250
Chrow Island	50
Chup Point	100
Cigarette Cove ^a	300	5	0	150

Locality	Thousands of juvenile herring			
	1951	1952	1953	1954
Coaster Channel	10
David Channel	..	b	b	50
Diana Island	0
Dodger Channel	..	1	10	50
Dutch Harbour ^a	..	200	0	150
Ecoole Cannery	..	300	0	500
Edward King Island	0
Effingham Inlet	300	3	1	600
Effingham Island	..	200	5	1,000
Fleming Island	75
Forbes Island	0
Georges Island ^a	c	c	c	250
Grappler Inlet	d	d	d	200
Hand Island Channel ^a	..	100	..	500
Harris Point	0	0	400	80
Helby Island	0
Island Harbour	..	500	0	50
Island Harbour to Coaster Channel	30
Jaques Island	0
Jarvis Island	0
Kelp Bay ^a	35	2,000
Kelp Bay ^a to Danvers Inlet	1,000
Loudoun Channel	2,000
Macoah Passage	1,000
Mayne Bay	10	0	0	2,000
Nanat Islet	0
Nanat Islet to Danvers Islet	30
New York Point ^a	200	c	c	200
Numukamis Bay	150
Ohiat Island	0
Peacock Channel	300
Pipestem Inlet	500	5	1,010	1,500
Rainy Bay	..	20	0	300
Rainy Bay to Vernon Bay	0
Ritherdon Bay	0
San Mateo Bay	..	1,000	300	1,000
Sarita Bay ^a	10	1,100
Satellite Passage	..	50	0	100
Sechart Channel	100	1,000	15	1,000
Snowden Island	e	c	c	500
Snug Basin	30
Stopper Islands	35	5	10	700
Swaile Rock	e	e	e	70
Swaile Rock to Island Harbour	..	e	e	50
Thiepval Channel	1,000
Toquart Bay	400	0	0	250
Turtle Island	0
Tzartes Island (east side)	2,000	0	500	1,000
Tzartes Island (west side)	..	f	f	100
Uchucklesit Inlet	400	5,000	300	900
Ucluelet Inlet	80	300	100	1,000
Useless Inlet	300	1	200	300
Vernon Bay	30	250
Totals	5,660	10,043	7,611	24,975

^aLocal name

^bIncluded in Mayne Bay

^cIncluded in Toquart Bay

^dIncluded in Banfield Inlet

^eIncluded in Sechart Channel

^fIncluded in Tzartes Island, east side.

Estimates of the total population in the localities covered by the marking operation each year (Table XII) were made from the basic marking and recovery data (Tables I-IV). Confidence limits, based on random distribution of marks, were determined according to Ricker (1937). Since different stocks were

TABLE XII. Estimates of the abundance of juvenile herring in localities in Barkley Sound in which Schnabel-type marking experiments were carried out. Limits of confidence are based on the assumption of random mixing of marked and unmarked fish and may be too narrow insofar as this condition is not met.

Year	No. of fish marked	No. of fish examined	No. of recoveries	Population	
				Estimate	95% limits
All localities marked				<i>millions</i>	<i>millions</i>
1951	33,986	44,413	58	11.7	9.0- 15.2
1952	81,016	81,730	30	67.3	47.1- 99.9
1953	141,188	167,571	65	166.5	130.6-212.2
1954	163,350	179,170	59	188.3	147.1-239.9
Banfield Inlet					
1951	18,863	12,863	17	4.4	2.7- 7.5
1952	20,688	20,186	3	40.6	13.9-203.0
1953	46,011	44,911	26	41.6	28.5- 63.7
1954	26,060	24,770	7	43.5	21.2-108.8
Banfield Inlet and Kelp Bay					
1954	40,680	48,010	13	74.4	43.4-140.1
San Mateo Bay					
1952	20,884	21,567	8	16.9	8.5- 39.7
1953	30,541	38,177	7	71.2	34.6-178.0
1954	18,240	18,340	7	38.3	18.6- 95.9
Uchucklesit Inlet					
1953	14,460	16,488	3	41.1	14.0-205.4
1954	22,880	19,020	5	37.7	16.1-117.9
Ucluelet Inlet					
1952	8,852	9,202	3	5.2	1.8- 25.7
1954	26,840	22,050	9	27.3	14.4- 61.4
Useless Inlet					
1951	10,953	8,605	5	4.5	1.9- 14.2
1954	5,270	6,050	3	10.6	3.6- 53.1

marked in different years these total estimates are not directly comparable, with the possible exception of 1953 and 1954. These years have six localities in common. Markings and populations in the other localities were relatively small. The 1953 estimate should exceed that of 1954 for populations of comparable size, since it covers more of the total population of the sound. The 1954 estimate slightly exceeds that of 1953 and thus the 1954 juvenile herring population in Barkley Sound may have been larger than that of 1953. This is in accord with the estimates based on scouting.

A further indication of the relative strength of these year-classes may be derived from a comparison of local stocks whose abundance estimates were based on more than one recovery (Table XII). Estimates for all four years are available for Banfield Inlet, while 1952 to 1954 estimates are available for San Mateo Bay. The 1954 stocks in Uchucklesit Inlet, Ucluelet Inlet and Useless Inlet may be compared with those in 1953, 1952 and 1951 respectively.

The 1951 markings were not sufficiently extensive to enable adequate estimates. In addition techniques were in the process of development, and marking mortality was probably rather variable. The 1952 year-class appears to have been definitely weaker than the two succeeding ones in two of the three localities in which estimates could be made. The 1953 and 1954 year-classes were of comparable size in Banfield and Uchucklesit Inlets, while the 1953 year-class was stronger in San Mateo Bay.

Considering the results of both comparisons of relative abundance, the 1953 and 1954 year-classes appear to have been approximately equal in numbers, while the 1952 year-class was definitely smaller.

ABSOLUTE POPULATION ESTIMATES

An index of the extent to which a stock of juveniles was observed in a survey of a locality, may be obtained by comparing the population estimates from the marking experiments with the scouting estimates for these localities. The latter were invariably smaller, as even an extensive visual survey would not likely discover all the fish in a locality. Consequently the visual estimates for the entire sound must be low; the true level of abundance probably lies closer to that which could be obtained by marking extensively throughout the sound. Such a program was beyond the scope of this study but an approximation to this type of estimate was obtained by calculating an "adjustment factor" for the scouting estimates in the localities included in the marking program, and applying it to the scouting estimate for the sound (Table XIII). Thus the 1953 and 1954 year-classes in

TABLE XIII. Estimates of the 1951-1954 juvenile herring populations in Barkley Sound from the scouting survey coverage adjusted to the extent indicated by marking experiments.

Year	Estimate for localities marked		Adjustment factor	Estimate for Barkley Sound	
	From marking	From scouting		From scouting	Adjusted
	<i>millions</i>	<i>millions</i>		<i>millions</i>	<i>millions</i>
1951	10.91	2.00	5.5	5.66	31.1
1952	67.26	8.95	7.5	10.04	75.3
1953	166.50	1.97	84.5	7.61	643.0
1954	188.29	7.30	25.8	24.98	644.4

Barkley Sound apparently constituted about 640,000,000 fish in the juvenile stage. Coverage of the other two year-classes was not sufficiently complete to consider the estimates quantitatively.

CONCLUSIONS ON ABUNDANCE

Calculations based on recruitment and natural mortality rates (Appendix 4) show the average recruitment of the 1942-1952 year-classes would have been provided by a juvenile population of 403 million fish (ignoring the 1951 year-class which was not subject to a fishery at recruitment). The smallest year-class (1948) would have had a population of 269 million in the juvenile stage, whereas the largest year-class (1947) would have sprung from 575 million juveniles. On this basis, the 1953 and 1954 year-classes (about 640 million fish each) were well above average in strength. Although the coverage of the 1952 survey was not complete enough to permit comparison with the above determinations, it was sufficient to indicate that this year-class was appreciably weaker than the two succeeding year-classes.

The 1952 year-class was well below average strength when recruited to the 1954-55 fishery (Taylor, 1955) and the 1953 year-class was above average strength when it entered the fishery in 1955-56 (Taylor *et al.*, 1956). The 1954 year-class had an above-average recruitment as II-year fish and appears to be at least comparable to that of 1953. Thus, in general, relative abundance at recruitment appears to coincide with predictions based on juvenile abundance.

RELATIONSHIP OF JUVENILE HERRING STOCKS TO THOSE OF
THE EGGS AND LARVAE

DISTRIBUTION

The Barkley Sound juvenile herring stocks are concentrated in inlets and bays and around islands, mainly on the southeast side of the sound (Fig. 4). However, spawning occurs mainly on the opposite side of the sound. Thus, either there is high mortality in the spawnings along the northwest side and low mortality in the spawnings along the southeast side, or a large portion of the fish migrate across the sound sometime before mid-summer. The first alternative seems unlikely since:

(1) There is no evidence of such differential mortality either in the egg or larval stages. Larvae are considerably more abundant on the northwest side of the sound (Stevenson, 1955a).

(2) Some juvenile stocks on the northwest side (e.g. Toquart Bay), and in the middle of the sound (Broken Group) disappeared early in the summer. Recoveries of marked fish in these stocks were taken mainly along the southeast side, indicating migration in that direction.

(3) At least some (Banfield Inlet, San Mateo Bay) of the stocks along the southeast side appear to contain numerous size-groups, presumably reflecting the age differences involved in the hatchings from several spawnings. Since the number of these size-groups could not be accounted for by the number of spawnings along the southeast side (4 to 7), but could be accounted for by the number of spawnings on the northwest side (9 to 12) or in the sound as a whole (13 to 19), migration from the northwest to the southeast side is indicated.

Thus, the juvenile stocks located apparently arise from the hatchings of spawn throughout the sound and not just local spawnings. Sometime prior to the intensive schooling stage of juveniles in mid-summer, a large portion of the

young herring migrate from the northwest to the southeast side of the sound. Since the larvae are more abundant on the northwest side up to the late post-larval stages, after which they can escape capture by plankton nets, this movement must take place during or shortly after metamorphosis.

ABUNDANCE

The juvenile herring population in Barkley Sound has been estimated in excess of 640 million fish (minimum estimate from surveys and marking programs) in the two years for which adequate data are available. How many eggs and larvae would be required to produce this population? Since it appears that mixing among the various hatchings was relatively extensive prior to mid-summer, the population for the entire sound is treated as a unit.

Estimates of the length, width and intensity of spawn depositions are available from the reports of the Department of Fisheries in this area, and from special surveys made by scientists of the Fisheries Research Board of Canada (Taylor and Outram, 1954, and other reports in this series). From these reports the area covered by spawnings of each intensity can be calculated. These estimates, particularly of intensity, are rather rough but they permit an estimate of the number of eggs deposited after the method outlined by Hourston (1953b). Estimates for 1951 to 1954 were 417, 404, 335 and 476 billions (Table XIV). Thus, about 400 billion eggs were deposited annually over the 4-year period of this study. Mortality in the egg stage has been estimated at 65% (Stevenson, 1955b) and during the larval stage at 99.5% (Stevenson, 1955a). Applying these rates to the above egg estimates:

Number of eggs = 400,000 million

Number of newly-hatched larvae = 140,000 million

Number of metamorphosed juveniles = 700 million

Agreement of the juvenile estimate with the 1953 and 1954 survey estimates (640 million) is striking. The 700 million estimate should be high, as it includes no mortality during the early juvenile stage, whereas the 640 million may be low because some small stocks may have remained undetected. However the 1953 and 1954 year-classes are thought to be above average in size and consequently the average juvenile population may be somewhat less than 600 million fish. Thus Stevenson's mortality estimates may be slightly low, but an absolute error of 0.1% in larval survival or 9% in egg survival (either of which is not unreasonable) would account for the difference in estimates.

SUMMARY AND CONCLUSIONS

The population dynamics of the Pacific herring in the juvenile (first year) stage were investigated in Barkley Sound on the west coast of Vancouver Island during the summer months of 1951 through 1954. The primary objective was the assessment of relative population size in the juvenile stage with a view to predicting recruitment to the fishery 2 years later. This information, of importance in efficient management of the fishery, forms an integral part of special population studies now in progress on Pacific herring in British Columbia waters. In order

TABLE XIV. Area and intensity of herring spawnings in Barkley Sound, 1951-1954. Estimates of the number of eggs involved were obtained using the best available data on the average number of eggs per acre for each intensity category.

Date	Place	Area of spawn	Spawning intensity	Number of eggs
1951		<i>acres</i>		<i>millions</i>
Feb. 11	Macoah Passage	26.03	L	33,266
Feb. 15	Banfield Inlet	1.32	VL	45
Feb. 15	Useless Inlet	4.65	VL	158
Mar. 8	Mayne Bay	.26	VL	9
Mar. 8	Toquart Bay	33.69	M	164,542
Mar. 10	Banfield Inlet	1.24	VL	42
Mar. 12	Macoah Passage	24.79	VL	842
Mar. 12	Macoah Passage	2.48	VL-L	1,627
Mar. 15	Forbes Island	1.05	L	1,342
Mar. 16	Useless Inlet	4.34	M	21,197
Mar. 17	Kelp Bay	0.31	VL	11
Mar. 26	Toquart Bay	1.24	M	6,056
Apr. 1	Snowden Island	0.14	L-M	431
Apr. 2	Toquart Bay	28.23	H	187,052
Total for 1951		129.77		416,620
1952				
Feb. 8	Macoah Passage	6.65	VL	226
Feb. 10	Banfield Inlet	4.21	VL	143
Feb. 28	Useless Inlet	8.81	L	11,259
Feb. 29	Macoah Passage	3.95	L	5,048
Mar. 1	Kelp Bay	2.07	M	10,110
Mar. 6	Toquart Bay	9.09	M	44,396
Mar. 10	Grappler Inlet	1.18	M	5,763
Mar. 11	Macoah Passage	6.52	M	31,844
Mar. 14	Toquart Bay	20.21	L-M	62,267
Mar. 17	Banfield Inlet	5.58	L-M	17,192
Mar. 17	Macoah Passage	34.00	M	166,056
Mar. 25	George's Island	5.25	M	25,641
Mar. 25	Snowden Island	1.90	M	9,280
Apr. 9	Hillier's Cove	0.99	M	4,835
Apr. 9	Toquart Bay	2.09	M	10,208
Total for 1952		112.50		404,268
1953				
Feb. 22	Macoah Passage	18.90	L	24,154
Feb. 24	Banfield Inlet	1.13	L	1,444
Feb. 24	Mayne Bay	0.52	VL	18
Feb. 24	Useless Inlet	0.47	M	2,295
Mar. 1	Macoah Passage	0.47	VL	16
Mar. 1	Useless Inlet	8.06	VL	274
Mar. 2	Toquart Bay	64.57	VL	2,195
Mar. 7	Macoah Passage	3.72	L	4,754
Mar. 9	Banfield Inlet	24.38	M	119,072
Mar. 9	Macoah Passage	3.49	VL	119
Mar. 10	Kelp Bay	0.09	H	596
Mar. 16	Toquart Bay	64.95	L	83,006
Mar. 20	Useless Inlet	73.70	VL	2,506
Mar. 23	Snowden Island	0.83	VL	28
Mar. 26	Banfield Inlet	1.24	M	6,056
Mar. 27	Hillier's Cove	1.61	M-H	9,266
Mar. 28	Macoah Passage	5.81	L	7,425
Mar. 28	New York Point	.52	VL	18
Mar. 30	Stopper Islands	10.85	H	71,892
Total for 1953		128.48		335,134

Date	Place	Area of spawn	Spawning intensity	Number of eggs
1954		<i>acres</i>		<i>millions</i>
Feb. 26	Toquart Bay	14.46	VL	492
Feb. 27	Roquefeuil Bay	1.76	M	8,596
Mar. 3	Macoah Passage	59.30	L	75,785
Mar. 5	Useless Inlet	6.20	L	7,924
Mar. 9	Toquart Bay	21.59	L	27,592
Mar. 10	Useless Inlet	13.00	L	16,614
Mar. 15	Macoah Passage	28.20	M	137,729
Mar. 17	Rainy Bay	.41	L	524
Mar. 18	Snowden Island	.83	L	1,061
Mar. 19	New York Point	9.92	M	48,449
Mar. 28	Banfield Inlet	29.44	M	143,785
Mar. 28	Toquart Bay	.83	L	1,061
Mar. 29	Hermit Island	.98	H	6,493
Apr. 3	Useless Inlet	.10	VL	3
Apr. 14	Toquart Bay	7.81	VL	266
Total for 1954		194.83		476,374

to assess the abundance of juveniles in Barkley Sound, an important rearing ground, it was first necessary to determine there the distribution of the population and its composition. Relating the results of this study to studies on the preceding (larval and egg) stages permits their application to general population studies. These objectives may now be considered in the light of the data presented on the population of juvenile herring in Barkley Sound.

DISTRIBUTION OF THE JUVENILE HERRING IN BARKLEY SOUND. Scouting, seining and light fishing programs indicated that the juvenile herring in Barkley Sound live mainly in the shallow and protected waters in bays and inlets, and around islands. Some relatively large groups occur offshore, especially in the late summer and fall when the fish begin to move to offshore feeding grounds, but these fish appear to be transients.

COMPOSITION OF THE JUVENILE HERRING POPULATION. On the basis of results from a marking program and a study of differences in size-groups present in samples, the Barkley Sound juvenile herring population appears to comprise a number of individual stocks that mix somewhat, but not enough (less than one-third of the stock emigrating) to destroy their identity. Emigration is generally to adjacent and nearby localities but some fish wander to distant parts of the sound. Most of these fish remain on the same side of the sound rather than moving to the other side, possibly indicating that they customarily follow the shore rather than venturing into deep waters. The extent of migration appears to be directly related to distance moved, decreasing by about one-fifth to one-half for each additional 5 miles.

ABUNDANCE OF JUVENILE HERRING. Estimates of the relative abundance of juveniles were made during each scouting survey. Absolute juvenile abundance was estimated for several localities each year by Schnabel-type marking experiments, and these estimates were compared with those obtained by scouting for the same localities to arrive at a "correction factor" for the scouting estimates. The correction factor for each year was then applied to the scouting estimate for the entire sound. The results indicate that the 1953 and 1954 juvenile populations

were apparently in excess of 640 million fish (the minimal estimates). Two additional independent estimates of average year-class strength at the juvenile stage were based on extent of spawn deposition and mortality during the egg and larval stages, and on recruitment and mortality between the first summer and maturity. These rough estimates of 700 million and 403 million juveniles respectively compared rather well with the direct estimate. Relative juvenile abundance indicates that the 1953 and 1954 year-classes are above average in strength whereas the 1952 year-class is below average. The results of the 1953-54 and 1954-55 fisheries support this conclusion, indicating that this method of predicting recruitment has practical value.

ORIGIN OF THE STOCKS OF JUVENILE HERRING (relationship to earlier stages in the life history). Each local stock of juvenile herring in the sound apparently comprised the progeny of several hatchings as each contained several size-groups. The majority appear to have been hatched on the northwest side of the sound, as most of the spawnings took place there and the number of size-groups in samples from the southeast side could not be accounted for by the spawning on the southeast side. The larger portion of the progeny from the spawnings on the northwest side presumably migrated to the southeast side early in the summer, as fish marked in stocks which disappeared from the northwest side during June and July were recovered on the southeast side. Also there were relatively few stocks located on the northwest side. Extensive mortality in the egg (65%) and larval (99.5%) stages reduces a population of about 400,000 million eggs to about 700 million juveniles.

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APPENDIX 1: MARKING MORTALITY

A series of 14 experiments was carried out in order to determine the extent of mortality suffered by juvenile herring as a result of marking (Table A). Fish marked by removing fins, in the various combinations employed in the marking program, were placed in a live pound or tank along with "controls" (unmarked fish which had received minimal handling). The dead of each type were removed and counted every day. The probable percentage survival of the marked fish was taken to be the percentage survival of the marked fish plus the percentage mortality of the controls. This correction should allow for mortality due to causes other than marking, such as poor feeding conditions, disease and adverse environmental conditions. However, the controls were subjected to handling that would not occur under natural conditions (seining, transportation in a boat live pound, and transfer to the experimental pounds or tank), and to shock resulting from an abruptly restricted environment. Any fish noticeably suffering from this treatment were discarded, but probably some minor injuries escaped notice.

TABLE A. Survival of marked fish in mortality experiments. Corrected survival discounts mortality due to causes other than marking, as indicated by the survival of the control (unmarked) fish.

Experiment Number	Duration	No. of fish		Observed survival		Corrected survival of marked fish
		Controls	Marked	Controls	Marked	
	<i>days</i>			<i>%</i>	<i>%</i>	<i>%</i>
1	12	44	45	98	78	80
2	10	31	38	71	71	100
3	18	18	20	83	55	66
4	18	19	20	58	45	78
5	18	20	20	75	50	67
6	18	6	6	100	33	33
7	18	46	44	96	82	85
8	20	50	49	92	88	96
9	28	40	200	100	81	81
10	19	41	180	100	89	89
11	16	200	234	91	44	48
12	16	100	98	92	91	99
13	16	100	102	97	96	99
14	51	116	20	49	70	100+
Average					70	80

Handling mortality should be included in marking mortality. Presumably its major component is that resulting from picking the fish up in the hand and holding it out of water for several seconds during the marking. Chances of loss of scales and shock to the system are greatest at this point, and the fish would be expected to be damaged far more than during seining, transportation and transfer, provided these operations are carried out with due care. Consequently, the exclusion of these latter factors from marking mortality is not serious, especially since the average over-all mortality of the controls in good condition was only about 3% to 15%.

It seems reasonable, therefore, to consider the percentage mortality of the controls as representing the mortality due to causes other than the general marking operation, and thus to add this percentage to the percentage survival of the marked fish in order to estimate the probable survival of marked fish in nature, assuming that the marked fish are no more susceptible to predation than are the unmarked ones (Shetter, 1952).

Experiments 1, 7 and 8 were carried out in a "web" live pound similar to that employed in marking in the field ($3 \times 4 \times 5$ ft., of half-inch tarred web, Fig. 14A). Experiments 3, 4, 5 and 6 were carried out simultaneously in each of four chambers of a "box" type pound. This was a wooden box, $8 \times 2 \times 2$ ft., divided into four chambers, with stout quarter-inch wire

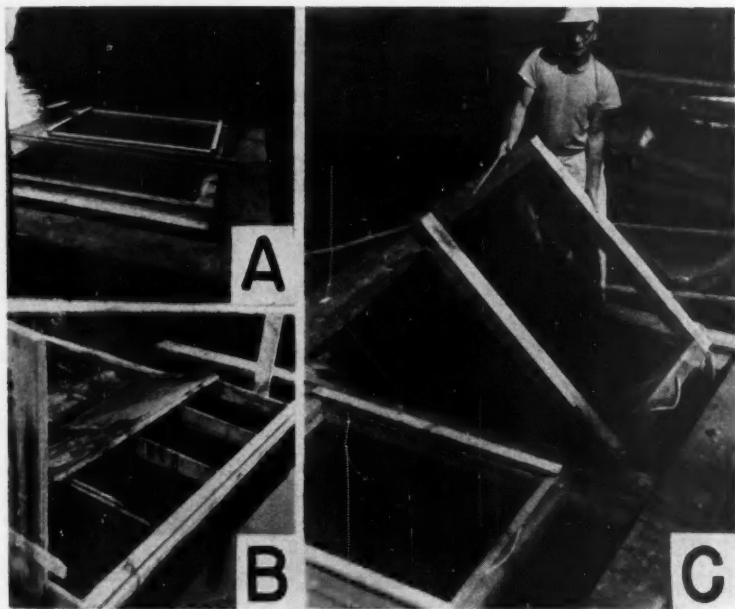


FIGURE 14. Live pounds used to hold fish for mortality experiments.

- A. "Web" live pound.
- B. "Box" live pound.
- C. "Wire" and "boat" live pounds.

mesh forming the two long sides of the box (Fig. 14B). All of these chambers were employed in Experiment 2. During the above experiments, the live pound was attached to the float at the Biological Station dock in Departure Bay. Although this location was relatively sheltered, the pounds were occasionally subject to considerable rocking, because the whole float moved with the stronger waves. Furthermore the water in the pounds was churned by the wash of boats coming into and leaving the dock. Consequently, for Experiments 9 to 13 the location was shifted to a specially constructed float anchored in the lee of a small island in Departure Bay. These experiments were carried out in a "wire" live pound, a structure similar to the "web" pound, but with wire mesh substituted for the web (Fig. 14C). This substitution was necessary as the web rotted quickly under constant immersion and was difficult to scrub clean of growth.

Experiment 14 was conducted in a circular laboratory tank, with a diameter of 37 inches and a depth of 22.5 inches (Fig. 15A). It was supplied with a constant flow of sea water. Survival conditions in this tank were checked by two control experiments. During the first check the methods of introducing new water and draining off the overflow were modified. In the final arrangement, the water flowed in through five holes, punctured by a 2-inch nail, on one side of a plastic tube inserted vertically in the tank about midway between the edge and the center (Fig. 15B). The inflow of approximately 3.5 litres per minute resulted in a slow circular movement of water around the tank. The overflow spilled into a 1½-inch or 32 mm. (outside diameter) pipe in the centre of the tank, rising 20 inches (50 cm.) from the drain on the bottom. This free overflow facilitated the escape of the scum that collected at the surface (mainly from the food given to the fish).



FIGURE 15A. Photograph of the laboratory tank used to hold fish during mortality experiments.

Juveniles seined in Departure Bay were transferred to a "boat" live pound (an old 12-foot dinghy with a large number of small slits, $1\frac{1}{2} \times \frac{1}{4}$ inch or 38×6 mm., cut in the bottom) for transport to the Biological Station dock, about a quarter of a mile away. The fish were carried in bait pails from the dock to the laboratory, about 500 ft., where they were transferred into the circular tank.

The fish used in laboratory experiments were fed finely ground beef liver twice a day during the week and once a day on weekends. They did not feed for the first 2 or 3 days in either of the control experiments, but fed actively thereafter, breaking their school (orientated to the flow within the tank) immediately after encountering the liver. In spite of this regular feeding activity and a controlled environment, the herring died at the rate of about one a day for the first three weeks of the first control experiment. After the 21st day of the experiment, the liver diet was supplemented with brine shrimp. The bulk of the diet was still provided by ground liver, but the inclusion of one quart of brine shrimp culture in each feeding seemed to relieve some diet deficiency, since only one death occurred in the next ten days. On the 31st day, a failure in the water pump resulted in death of all the juveniles. Throughout the second control experiment, the water exchange was as outlined above, and the juveniles were fed ground liver supplemented by brine shrimp. Two of the 157 juveniles died the first day, presumably as a result of injury during transit, but no further mortality was observed that week. Rearing conditions were then considered suitable and the mortality experiments begun.

Survival was extremely variable between experiments (Table A). In the earlier experiments this probably reflected the skill of the markers and the variability of conditions in the box pound. Since the fish used in Experiment 11 seemed rather sluggish at the time of marking, this experiment cannot be considered representative. Ignoring the box pound experiments and Experiment 11, all of which were probably atypical, the average corrected survival was 91%. Thus mortality due to marking was probably less than 10%. Indeed in the tank experiment, where rearing conditions were best controlled, the mortality of the marked fish was less than that of the fish used as controls. In the two experiments which were carried out in the wire pound in 1953, marking mortality was only 1%. Since the skill of the markers and environmental

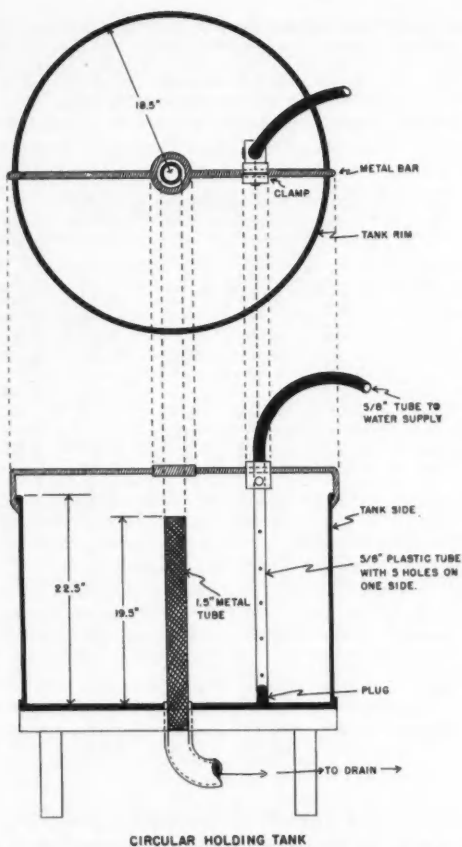


FIGURE 15B. Diagram of the laboratory tank used to hold fish during mortality experiments.

conditions probably approached conditions of field operations most during these latter three experiments, marking mortality may be considered negligible. In any case it is probably less than the 9% average for the web and wire pound experiments (ignoring Experiment 11).

APPENDIX 2: SAMPLING TECHNIQUE

Various checks were employed from 1952 through 1954 to test randomness in selection of fish preserved as a sample, randomness in selection of fish to be measured and weighed from the preserved sample, and average weights for the samples.

RANDOMNESS OF SELECTION OF FISH FOR SAMPLE

Nine times, a catch was sampled in duplicate (Table B). Five of the 9 pairs of samples show length differences of less than 1%, two show less than 2%, and two show less than 4%. Consistent biases are lacking. It may therefore be assumed that the fish taken from the catch as a sample are representative of it.

TABLE B. Average length and weight of fish in nine duplicate samples used to check sampling technique. Average weight was determined (1) from the sums of the individual weights (column 7); (2) from the weight of the sample as a whole (column 8); and (3) from the weight, as a whole, of the remainder of the fish after 100 had been sampled (column 9). The average weight employed (column 10) was the mean of the first two determinations.

1	2	3	4	5	6	7	8	9	10
Sample number	Date	Locality	No. of fish	Average length	Difference	Average weight			
						Individuals	Sample	Remainder	Average
						mm.	g.	g.	g.
52-59A	27/8/52	San Mateo	123	81.42		6.94	6.82	6.87	6.88
52-59B		Bay	123	82.61	1.19	7.50	7.38	7.35	7.44
53-37A	22/7/53	Banfield	312	58.84		2.34	2.27	2.24	2.31
53-37B		Inlet	340	58.11	0.63	2.22	2.18	2.12	2.20
53-39A	29/7/53	Uchucklesit	375	53.34		1.73	1.70	1.72	1.72
53-39B		Inlet	390	53.22	0.12	1.72	1.71	1.65	1.72
53-43A	30/7/53	Banfield	287	64.13		3.13	3.21	2.38	3.17
53-43B		Inlet	292	62.26	1.89	2.94	2.90	2.82	2.92
53-44A	30/7/53	Banfield	256	69.93		3.81	3.75	3.54	3.78
53-44B		Inlet	242	67.32	2.61	3.71	3.72	3.45	3.72
53-67A	7/8/53	Vernon	213	52.33		1.71	1.63	1.63	1.67
53-67B		Bay	240	53.81	0.48	1.72	1.69	1.68	1.71
53-83A	14/8/53	Uchucklesit	178	57.63		2.04	2.06	2.01	2.05
53-83B		Inlet	156	57.18	0.45	1.98	2.00	1.97	1.99
53-84A	14/8/53	Uchucklesit	425	58.20		2.14	2.20	2.15	2.17
53-84B		Inlet	220	58.04	0.16	2.20	2.15	2.18	2.18
53-102A	25/8/53	Ucluelet	310	62.25		2.79	2.73	2.71	2.76
53-102B		Inlet	318	62.58	0.33	2.93	2.81	2.89	2.87

RANDOMNESS OF SELECTION OF 100 FISH FROM THE SAMPLE FOR WEIGHING AND MEASURING

This was checked by weighing the remainder of the fish preserved as a unit (when there were more than 20 extra fish), calculating the mean weight of these fish, and comparing this average with a similar determination for the 100 fish selected. In 138 such comparisons, the sample weights were greater 85 times, the remainder weights greater 48 times, and the weights equal 5 times. The average difference in sample and remainder average weights was 2.7% (0.101/3.718) of the average weight for all samples. In 1952 this average difference was 0.1% (0.006/5.113), in 1953 it was 3.3% (0.090/2.700) and in 1954 it was 4.8% (0.184/3.788). Thus although the error involved here is slightly greater than that involved in the selection of a sample, and shows a slight bias toward larger fish, it is relatively small for most samples and may be considered insignificant. Indeed, the two sets of determinations of average weight, when compared by "t" tests, showed no significant differences (1952, $P > 0.9$; 1953, $P > 0.6$; 1954, $P > 0.3$; all years, $P > 0.6$). When, occasionally, the individual errors were high (up to 17%) some selection was unavoidably introduced because a considerable proportion of either the larger or smaller fish were so damaged while being captured that they could not be measured.

ACCURACY OF AVERAGE WEIGHT DETERMINATION

Individual fish were weighed to the nearest 0.05 gram. This involves an error of 2% over the average weight range, but it can reach 10% in samples of smaller fish. Any consistent bias

in recording weights approximately intermediate between two weight classes could thus have a significant effect on the sample average. To check for such errors, a comparison was made, for all samples of over 20 fish, between the average weight determined from the sums of the weights of the individual fish and the average weight determined by an immediately subsequent weighing of the entire sample. In 183 such comparisons, the average determined from the total of the individual weights was larger 108 times (59%), smaller 63 times (34%), and there was no difference 12 times (7%). The average excess of one determination over the other was 0.91% (0.034/3.718) of the average weight for all samples. In 1952 this average difference was 2.02% (0.103/5.113); in 1953, 0.26% (0.007/2.700); and in 1954, 0.11% (0.004/3.788). Thus, although there was a slight tendency for the average from the total weight to be larger than that for the sample weighed as a unit, this difference scarcely exceeded the accuracy limit of the initial measurements and was not significant. The two sets of determinations of average weight when compared by "t" tests showed no significant differences (1952, $P > 0.8$; 1953, $P > 0.9$; 1954, $P > 0.9$; all years, $P > 0.8$).

APPENDIX 3: RELATIONSHIP OF LENGTH GROUPS IN SAMPLES TO MAJOR SPAWNINGS

The analysis by probability plots of length-frequency distribution of juvenile herring showed the presence of more than one length group in most samples. If the description of these size groups is valid, the size differences must be related to some biological cause. The most obvious explanation is an age difference. If this is so, the number of size-groups should be related to the number of distinct spawnings within the locality. An investigation of this relationship is feasible only in relatively isolated localities where mixing with other sub-populations is negligible. The juvenile herring population in Departure Bay seems to satisfy this prerequisite.

Major herring spawnings in the Departure Bay vicinity over the period of 1950 to 1953 were compared with the length-groups in the juvenile samples (Hourston, 1956). In 1950 the major spawnings were on March 7-11, March 20-29 and April 4-9. Length-frequency analysis shows two size-groups consistently present, with one more in several samples. One sample indicated an additional size-group, perhaps comprising strays, or, more likely, being an unreal product such as occasionally arises in a graphic analysis of this nature. It would thus appear that one size-group was present for each major spawning. In 1951, major spawnings were on March 8-11, March 16-19 and March 26. In the juvenile stocks that year, two size-groups were persistently present and a third size-group was indicated in several samples. Here again the number of evident size-groups in the juvenile stocks corresponds with the number of major spawnings. Similarly, in 1952 there were three evident size-groups and three major spawnings (March 6, March 9 and March 15). In 1953 two persistent size-groups and an additional quite evident one were produced from three major spawnings (March 8, March 17-21 and April 8).

It would thus appear that these size-groups are due to the age differential resulting from spawnings at different times. This graphic analysis, therefore, probably detects real differences.

APPENDIX 4: AVERAGE JUVENILE HERRING POPULATION AND POPULATION RANGE IN BARKLEY SOUND DETERMINED FROM CONTRIBUTIONS OF THE 1942 TO 1951 YEAR-CLASSES TO THE POPULATION OF ADULT HERRING

The contribution of a year-class to the adult herring population is measured from the number of fish of that year-class which are caught during and prior to the year in which the majority of recruitment occurs, plus the number that spawn in that year, plus the number remaining immature. For the lower east coast of Vancouver Island it was estimated that 74.9%

of the fish are recruited to the spawning population at age 3-,¹ with 0.4, 7.5 and 17.2% recruitment at ages 1-, 2- and 4-, respectively (Tester, 1955). Thus, 82.8% of the stock is recruited by age 3-. Since the population on the west coast of Vancouver Island is similar in age composition to that on the lower east coast of Vancouver Island, these percentages should apply generally to the Barkley Sound herring. Thus the contribution of a year-class at the major recruitment age 3- would be:

$$C_3 + B_3 + C_2 s_{2-3} + C_1 s_{1-3} + \frac{C'_4 + B'_4}{s_{3-4}}$$

where C = catch at age indicated in the subscript

C'_4 = catch of fish vulnerable for the first time at age 4-

B_3 = spawners at age 3-

B'_4 = fish spawning for the first time at age 4-

s = fractional survival between the ages indicated in the subscript

Estimates of the new recruits at age 4-, ($C'_4 + B'_4$), are not available, but could be derived from the age 3- estimates by applying the recruitment rates given above. However, a more straightforward and probably equally accurate determination for the total strength of a year-class at age 3-, ignoring the minor effects of the fishery on 1st-year fish (less than 0.2%), would be approximated by:

$$N_3 = \frac{C_3 + B_3 + C_2 s_{2-3}}{R_3}$$

where $R_3 = 0.828$, the fraction of recruitment completed by age 3-, and $s_{2-3} = 0.748$. Estimates determined in this way were tabulated for the 10-year period represented by the 1942-52 year-classes, omitting the 1950 year-class because of the lack of a fishery in its recruitment year (Table C).

TABLE C. Estimation of the potential population of 3rd-year fish (N_3) resulting from the 1942-1952 year-classes, using the formula $N_3 = \frac{C_3 + B_3 + C_2 s_{2-3}}{R_3}$, where $R_3 = 0.828$ and $s_{2-3} = 0.748$.

Year-class	C_3	B_3	C_2	Potential N_3
1942	23.07	167.06	27.78	254.78
1943	151.63	62.78	20.82	277.82
1944	116.88	60.20	15.74	228.13
1945	145.50	41.84	8.45	237.57
1946	123.06	80.73	33.84	276.75
1947	182.04	97.52	12.31	348.83
1948*	63.60	25.99	15.22	121.97
1949	69.92	50.90	5.60	151.01
1951	187.61	69.30	0	310.28
1952	83.09	103.50	7.89	234.88
Average	114.64	76.28	16.41	244.20

*There was no fishery in 1952, when these fish would normally have become adult. For this year-class the estimate was obtained from catch plus spawning at age 4-, allowing for natural mortality of 38% (Fig. 16A; $q = i = 0.48$ and $m = a = 0.38$ where q and i are the instantaneous natural and total mortality rates and m and a are the annual natural and total mortality rates).

¹"Age 3-" refers to fish in their third year of life, mostly taken between November and February; they have completed their third season of growth, but are not yet a full 3 years old, having been hatched in March or April.

Stevenson (1955c) used a natural mortality rate for British Columbia herring of 50% per year "in the absence of contradictory evidence" over the period from year 1 to recruitment during year 3 (he considered natural mortality rate to be constant over the life span of the metamorphosed fish). However, Tester (1955) has shown that natural mortality increases with age at least after recruitment, and, presumably, before recruitment also. In addition, on the basis of Stevenson's mortality rates, the average juvenile population over the period from 1942 to 1951 would have been 777 million with a low of 488 million (1948) and a high of 1,395 million (1947). But the 1953 and 1954 juvenile populations (640 million) would have been well below average under these circumstances, whereas reports on relative abundance indicate that they were above average. Thus Stevenson's natural mortality rates for this period are probably high.

An alternative estimate of the juvenile populations associated with the recruitments given above may be derived from Tester's (1955) estimates of instantaneous mortality between the first year and recruitment. The number of juveniles required to produce a given recruitment as age 3- fish is given by:

$$N_1 = \frac{N_3}{s_{1-3}} \quad (1)$$

where N_1 = number of 1st year fish

N_3 = number of 3rd year fish

s_{1-3} = survival from 1st year to 3rd year.

$$s_{1-3} = e^{-i_{1-2} - i_{2-3}} \quad (2)$$

where i_{1-2} = total instantaneous mortality from the 1st to the 2nd year

i_{2-3} = total instantaneous mortality from the 2nd to the 3rd year.

$$i = p + q \quad (3)$$

where p = instantaneous mortality from fishing

q = instantaneous mortality from natural causes.

Extrapolation of curves drawn by Tester (1955) gives values of 0.12 and 0.25 for q_{1-2} and q_{2-3} respectively for the herring population on the lower east coast of Vancouver Island. Tester states that, in general, estimates of natural mortality in Area 23 (Barkley Sound) would be similar. Although Tester's data came from recruited fish, which may behave differently in this respect, and although the trend could change in the early age range, the extrapolations do not appear grossly unreasonable from general considerations.

Over the period 1946-47 to 1953-54 the percentage in the catch of fish in their second year was approximately 0.0004.

Thus $i_{1-2} = q_{1-2} = 0.12$ (since p_{1-2} is negligible); and $i_{2-3} = q_{2-3} + p_{2-3}$. Now p_{2-3} is a function of μ_{2-3} , which is the rate of exploitation by the fishery during the second year of life, and of q_{2-3} , which is the natural mortality rate for the same period. Putting C_2 for catch in year 2:

$$\mu_{2-3} = \frac{C_2}{N_2} = \frac{C_2}{N_3/s_{2-3}}$$

$$\frac{C_2}{N_3} = (s_{2-3}) (\mu_{2-3})$$

Putting total annual mortality equal to a :

$$\frac{C_2}{N_3} = (e^{-i_{2-3}}) \left(\frac{a}{i} \right)_{2-3} (p_{2-3})$$

Now C_2 = average number of 2nd year fish in catch over the period
 = 16.41×10^6 for 1942-43 to 1951-52 in Barkley Sound
 (from basic data)

N_3 = average number of 3rd year fish in the population
 (catch + potential spawners over the period)
 = 244.20×10^6 for 1942-43 to 1951-52 in Barkley Sound
 (from basic data)

$q_2 = 0.25$ according to Tester (1955)

To obtain the C_2/N_3 ratio of 0.0672 when $q_2 = 0.25$, p_2 must be 0.12.

From (3), $i_{2-3} = 0.25 + 0.12 = 0.37$, and $i_{1-3} = 0.12 + 0.37 = 0.49$.

From (2), $s_{1-3} = 0.61$; from (1) $N_1 = 400$.

Similar data for the smallest and largest year-classes are shown below:

	Smallest year-class (1948)	Largest year-class (1947)
N_3	121.97×10^6	348.83×10^6
C_2	15.22×10^6	12.31×10^6
C_2/N_3	0.125	0.0353
q_{2-3}	0.25	0.25
p_{2-3}	0.27	0.06
i_{2-3}	0.52	0.31
i_{1-3}	0.12	0.12
s_{1-3}	0.64	0.43
s_{1-3}	0.53	0.65
N_1	230×10^6	537×10^6

Thus, using Tester's estimate of natural mortality the average annual recruitment from 1942-43 to 1951-52 would have been produced by a juvenile population of 400 million fish. The smallest year-class (1948) would have been produced by 230 million juveniles and the largest (1947) by 537 million juveniles.

The 1953 and 1954 year-classes were estimated at about 640 million fish in the juvenile stage. Although these year-classes may be above average in strength, consistent local reports on relative abundance of juveniles in 1947 indicate that the 1947 year-class was definitely larger. Since the estimates made at the juvenile stage in 1953 and 1954 are considered minimal, the juvenile population estimates made above from recruitment and natural mortality data are probably low. Indeed the estimate of q between the first and second year seems remarkably low (0.12). Tester has questioned the validity of applying his extrapolation to the unrecruited age groups.

Tester (1955) also gives estimates for q for Areas 23 and 24. Since the Area 23 fish make up over 90% of this stock (Stevenson *et al.*, 1952, and previous reports in this series), Tester's estimates should apply very well to Barkley Sound. Plotting these estimates (Fig. 16A), and following Tester's procedure, a line was drawn through the values representing age 5- to 6- and 6- to 7-. This line also went through the point representing age 4- to 5- but did not go through the point representing age 7- to 8-. However, the latter point was the least reliable

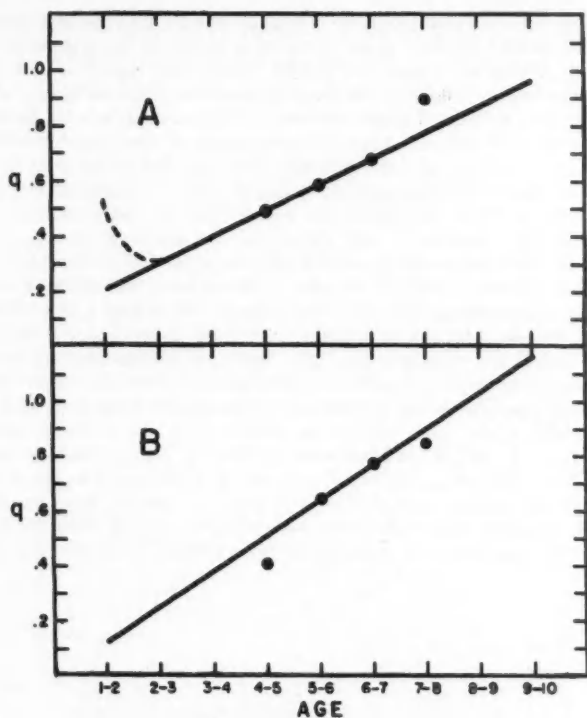


FIGURE 16. The relationship of instantaneous natural mortality (q) to age for each year in the life of the herring.

A. Areas 23 and 24 on the west coast of Vancouver Island.

B. Lower east coast of Vancouver Island.

(Tester, 1955). This line differs in slope from the general case for the lower east coast employed by Tester (Fig. 16B) and does not go through the origin. Employing the q values determined from this graph the above calculations of N_1 were repeated, as shown below:

	Average 1942-51	Smallest year-class (1948)	Largest year-class (1947)
N_0	244.20×10^6	121.97×10^6	348.83×10^6
C_1	16.41×10^6	15.22×10^6	12.31×10^6
C_1/N_0	0.0672	0.125	0.0353
q_{2-3}	0.29	0.29	0.29
p_{2-3}	0.12	0.30	0.06
i_{2-3}	0.41	0.59	0.35
i_{1-2}	0.20	0.20	0.20
i_{1-2}	0.61	0.79	0.55
s_{1-2}	0.54	0.45	0.58
N_1	452×10^6	271×10^6	601×10^6

Thus, using natural mortality data from Areas 23 and 24 only, the average annual recruitment from 1942-43 to 1951-52 would have been produced by a juvenile population of 452 million fish. The smallest year-class (1948) would have been produced by 271 million juveniles and the largest (1947) by 601 million juveniles. These estimates, although higher than those calculated above, still appear relatively low in comparison with the direct estimates for 1953 and 1954 (640 million). Again the extrapolation of the natural mortality curve may not be justified. On the other hand the correction factors applied to the scouting estimates may be high if marking mortality was appreciably higher than the negligible amount determined experimentally. In any event, the differences between the two determinations are small considering the assumptions involved in each method and the sources of error.

Alternatively, an estimate of natural mortality from the first to the third year might be made from the estimate of 1953-54 juveniles (640 million), the 1942-51 average age 3- population ($N_3 = 244$ million) and the average age 2- rate of fishing, $p_2 = 0.12$. A two-year decrease from 640 to 244 million means $s_{1-3} = 0.38$, hence $i_{1-3} = 0.96$, hence $q_{1-3} = 0.96 - 0.12 = 0.84$. This is a considerably higher figure for instantaneous natural mortality rate than the combined figure 0.49 ($= 0.29 + 0.20$) obtained from the linear extrapolation in Figure 16A. Thus q may really be approximately stable at about 0.4 from ages 1- to 4-; or, more likely perhaps, it may reach nadir in the interval q_{2-3} , and be higher again among the younger fish (q_{1-2}). A possible combination which adds up to $q_{1-3} = 0.84$ is indicated by the dotted line of Figure 16A: $q_{2-3} = 0.30$ and $q_{1-2} = 0.54$. From the biological point of view, at age 2- to 3- herring are large enough that many predators can no longer swallow them, and are fast enough to escape others that could; while relatively few of them are as yet involved with the dangerous excursions and physiological stresses which accompany reproduction.

Density and Distribution of Young Sockeye Salmon (*Oncorhynchus nerka*) throughout a Multibasin Lake System¹

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ABSTRACT

Estimates of density (based on catch per unit effort with tow nets) of fingerling sockeye salmon populations in a large (174 sq. mile) multibasin lake system were carried out during 1955, 1956 and 1957. Density and distribution of fingerling sockeye throughout the lake system are related to density and distribution of the spawning parent populations. Discrete populations associated with discrete basins point to a limited dispersal as a result of the multibasin nature of the lake system. In one example, higher population density appears to result in greater dispersal.

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INTRODUCTION

LARGE, MULTIBASIN BABINE LAKE and connected Nilkitkwa Lake, a total lake area of approximately 174 square miles (450 sq. km.), provide nursery facilities for the progeny of 70% or more of the anadromous sockeye salmon which spawn in the Skeena River system of northern British Columbia. Each year the anadromous sockeye entering this lake system and utilizing its tributary spawning grounds spawn during the period late July to late October. The eggs hatch the following spring and the resulting fry enter the lake in May and June where they take up residence in the pelagial as zooplankton feeders. During the first year of life in the lake they are known as fingerlings or age 0 sockeye. In the following May and June most of them are believed to migrate seaward as yearling (age I) smolts. The proportion of yearling smolts in samples from the smolt runs of 1950-56 ranged from 98% to 100%, the remainder being two-year-olds (age II).

Each year since 1946 (except 1948) the Fisheries Research Board of Canada has enumerated the anadromous sockeye salmon entering the system to spawn

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by means of a counting fence on the Babine River below the outlet. Information on the distribution of these fish to the various spawning grounds of the system is available through the Department of Fisheries, whose area officer makes estimates of the number of spawners on the grounds by regular, frequent examination throughout the spawning period each year. At the outlet, the Fisheries Research Board has carried out an estimate of the number of seaward migrating smolts each year since 1951 by means of a mark and recapture method.

In addition to anadromous sockeye salmon, Babine Lake also has a freshwater form known as kokanee which, except that they have not migrated to sea and are of much smaller size at maturity, are indistinguishable from the anadromous form. Whether or not, or to what extent, the progeny of these freshwater sockeye migrate seaward is unknown. Available information on these land-locked sockeye salmon of Babine Lake is set forth in Appendix II.

Initial study of the lake life of young sockeye salmon in Babine and Nilkitkwa Lakes was carried out in 1955 (Johnson, 1956). This study showed an extremely non-uniform distribution of fingerling sockeye, which was related to the spawning ground distribution of the parent population of anadromous sockeye. Since then, during the May to November period of both 1956 and 1957, intensive study of Babine and Nilkitkwa Lakes has been carried out.

This paper presents an analysis of findings to date regarding the density of fingerling sockeye salmon populations in the various regions of Babine and Nilkitkwa Lakes and its relationship to the distribution and abundance of the spawning parent populations. Results are discussed and comparisons made as each additional year's findings are presented.

Two importantly related topics are dealt with in the form of two appendices: (1) an analysis of variability in the catch per unit effort data; and (2) a summary of what is known of the so-called kokanee of this nursery area, and the reasoning and evidence used in attempting to segregate fingerling kokanee from fingerling anadromous sockeye.

METHODS AND ASSUMPTIONS

Estimates of population density are based on catch per standard unit of effort with tow-net gear as described earlier (Johnson, 1956). As such, only the 1956 and 1957 catches which were the result of one standard unit of effort are specifically dealt with here; other catches, although yielding samples utilizable for growth studies, etc., are not presented. The catches used are further restricted to the following period of time in each of the years: from late June (after all the young sockeye are believed to have entered the lake and taken up residence in the pelagial) to the time in autumn when surface water temperatures fell below 7°C. (sometime after which, catchability consistently becomes drastically reduced). During the summer period in each year, catchability and mortality rate are believed and assumed to have been relatively constant. It is also assumed that catch per unit of effort was related proportionately to population density throughout; and, that fingerling sockeye salmon, whether progeny of anadromous sockeye or of the freshwater form, are equally catchable with the tow-net gear employed.

ESTIMATES OF POPULATION DENSITY. Conversion of catch per unit effort to fish per acre is based on catch per unit effort in a lake where the approximate population density was known (from estimates of fry entering and smolts leaving). As the only such example available, catch per unit of effort at Lakelse Lake in August–September, 1955, showed a 1 to 12 relation to the number of fingerling sockeye per acre. On this basis the factor 12 was used to convert August, 1955, catches at Babine–Nilkitkwa to fish per acre (Johnson, 1956). After 1955, there were small improvements in the method of towing; consequently, a somewhat smaller factor of 10 is used below in converting 1956 and 1957 catches to density in fish pre acre.

THE SPAWNING PARENT POPULATIONS

The anadromous sockeye salmon and kokanee which spawned in 1954, 1955 and 1956 were the parents of the fingerling sockeye populations of 1955, 1956 and 1957 with which this paper is concerned. Table I gives the number and distribution of spawning anadromous sockeye salmon for these years.

TABLE I. Estimates of anadromous sockeye salmon spawning on grounds tributary to and below Babine and Nilkitkwa Lakes, excluding jack sockeye (early maturing, age III, anadromous males). The sex ratio is approximately 50:50 in all cases. (Based on Department of Fisheries Forms B.C. 16, Salmon Stream Spawning Reports.)

Spawning area	Estimated number of spawning sockeye		
	1954	1955	1956
Tributary to Nilkitkwa Lake and the North Arm of Babine Lake:			
Lower Babine River	98,000	9,000	52,000
Upper Babine River	157,000	10,000	67,500
5 Mile Creek	300	100	...
9 Mile Creek	1,000	60	...
Subtotals	256,300	19,160	119,500
Tributary to Babine Lake south of Halifax Narrows:			
Morrison River	12,000	1,800	17,100
Fulton River	106,000	14,500	81,000
Tachek Creek	1,900	300	...
Sockeye Creek	900	500	...
Pierre Creek	17,000	4,000	18,000
Twin Creek	14,000	2,500	4,500
Pendleton Creek	1,100
Kew Creek	300
Donald's Creek	300
15 Mile Creek	25,000	3,200	23,000
6 Mile Creek	1,800	100	50
4 Mile Creek	2,200	400	400
Grizzly Creek (branch of Beaver River)	3,100	500	4,800
Subtotals	185,600	27,800	148,850
Totals	441,900	46,960	268,350

No definite estimates of the number of spawning kokanee are available; however, general information on their relative abundance and distribution is set forth in Appendix II. The number of kokanee spawning in 1954 appeared to be insufficient to contribute any significant proportion of the fingerling sockeye population of 1955; however, the much greater numbers of kokanee spawning in 1955 and 1956 are believed to have contributed significantly to the fingerling sockeye populations of 1956 and 1957 in regions south of Halifax Narrows. Only an insignificant portion of the kokanee in any of the years spawned north of Halifax Narrows.

REVIEW OF 1955 RESULTS

The preliminary study of 1955 (Johnson, 1956) indicated a total population of 45 to 72 million fingerling sockeye salmon inhabiting the Babine-Nilkitkwa nursery area during the period late August to mid-October, 1955. Two-thirds or more of these fingerlings appeared to be concentrated in Nilkitkwa Lake and the North Arm of Babine Lake (north of Halifax Narrows)—which is about 11% of the area of the combined lakes (Fig. 1). Table II summarizes the estimates: essentially all fingerlings were considered progeny of anadromous sockeye. The uneven distribution of fingerlings was related to an unequal distribution of the 1954 parent population of anadromous sockeye on tributary spawning grounds (Table I) and suggested a limited dispersal of fry from their points of entrance into the lake. This limited dispersal appeared to be a result of the multibasin nature of the lake system. The mean sizes of these fingerlings in mid-October, 1955, as shown in Table II of Johnson (1956), were approximately as follows:

<i>Region</i>	<i>Mean weight in grams</i>
Nilkitkwa Lake	1.1
North Arm: north half	1.4
North Arm: south half	1.7
South of Halifax Narrows	3.4

The apparent slower growth in regions of greatest population density suggested a cause-effect relationship.

TABLE II. Summary of the estimates of fingerling sockeye salmon in the Babine-Nilkitkwa nursery area in August-October, 1955 (Johnson, 1956, p. 703-704).

Region	Fingerling sockeye salmon	
	Number per acre	Total number
		<i>millions</i>
North of Halifax Narrows:		
Nilkitkwa Lake	4600 to 4750	5.5 to 5.7
North Arm of Babine	2850 to 4100	32.7 to 47.2
Subtotal		38.2 to 52.9
South of Halifax Narrows:	72 to 196	7.1 to 19.3
Total:		45.3 to 72.2

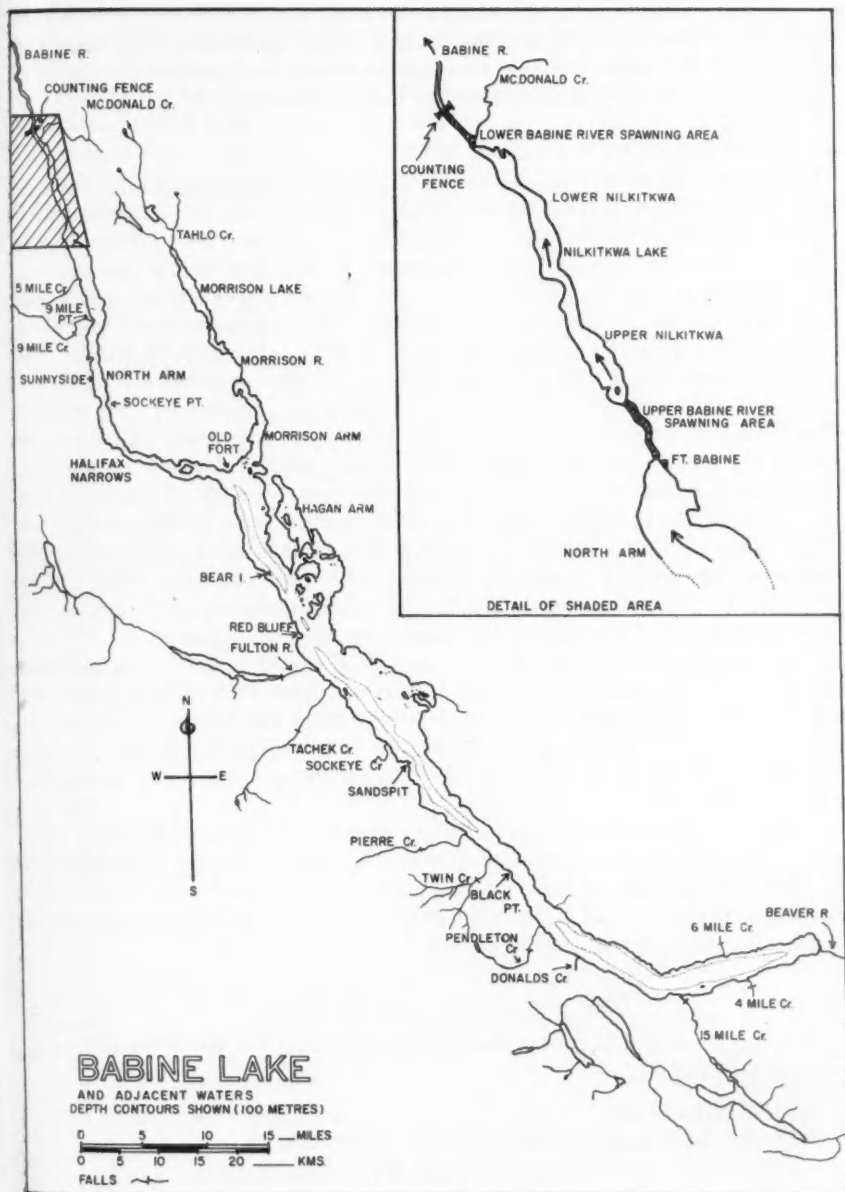


FIG. 1. Map of Babine Lake and adjacent waters.

Because of the very limited sampling in 1955, no precision could be claimed for the estimates of population density in any of the regions, or for the mean size of fish south of Halifax Narrows. However, evidence in support of the view that these estimates were reasonably accurate is now available.

SUPPORTING EVIDENCE

The estimate of the number of yearling (age I) smolts migrating seaward in the spring of 1956 was useful for a general evaluation of the preliminary findings of 1955: these smolts were the fingerling sockeye in lake residence during 1955. The estimate of this smolt exodus, made as described in the Introduction, was between 18 and 23 million. The seaward migration was already under way before estimation at the outlet by the mark and recapture method was commenced. Nevertheless, it is unlikely that the total exceeded 25 to 30 million. The age I smolts examined were of two distinct size groups; approximately 50% were very small (mean weight: 2.2 grams) as compared to the others (5.6 grams). Because the small group were the earliest to migrate, it is likely that the early part of the run missed by the estimate was made up largely of this group and that these small fish therefore constituted somewhat more than 50% of the total. The very small size of the earlier migrating smolts marked them as originating from regions north of Halifax Narrows. Regarding the total number of smolts migrating, from what is known of over-winter mortality elsewhere (Foerster, 1938), 20 to 30 million could be of the general order of smolt numbers expected from a lake population of 45 to 72 million in the autumn previous to migration.

Evidence concerning the origin of the small smolts is also available from tow-net collections throughout the lake in May and June, 1956. Although seaward migration was under way by the time these started and there was already a mixture of large and small smolts in Nilkitkwa Lake and the North Arm, catches from regions south of Halifax Narrows did not include the group of smaller yearling smolts.

Tow-net catches of yearlings in 1956 declined as the seaward migration progressed and afterwards yearlings were taken only rarely anywhere. This supports the view that progeny of kokanee made up an insignificant part of the total fingerling population of 1955—assuming of course that at least a significant portion of kokanee progeny do not migrate seaward.

THE FINGERLING SOCKEYE OF 1956

During the 1956 field season tow-net fishing was carried out in the following 6 regions (see Fig. 1):

- (1) Nilkitkwa Lake,
- (2) the North Arm between the outlet and 9 Mile Point,
- (3) the North Arm between Sunnyside and Halifax Narrows,
- (4) between Old Fort and Bear Island,
- (5) central Babine—between Red Bluff and Black Point, and
- (6) southern Babine—between Black Point and the south end.

No sampling was done in Morrison Arm or Hagan Arm; fingerling populations there are assumed to have been negligible because spawning adjacent to these arms was negligible.

Fingerling sockeye, progeny of 1955 spawning, were taken in small numbers as early as June 10, 1956; however, it is believed to have been late June before all such fry had entered the lake area and taken up residence in the pelagial.

Table III presents the 1956 catches of fingerling sockeye per unit of effort during the period from late June until the time in autumn when surface water temperatures fell below 7°C. and after which catchability was greatly reduced.

TABLE III. Catch per standard unit of effort of fingerling sockeye salmon, 1956.

Date 1956	Nikkitkwa Lake	Outlet to 9 Mile Pt.	Sunnyside to Halifax Narrows	Old Fort to Bear Is.	Central Babine	Southern Babine
July 2	13	...
4	...	5
5	270
15	0
16	...	5
17	93
18	0
19	0
20	0
22	35
23	26
24	17
31	154
Aug. 4	15	...
5	12	...
6	47	...
8	0
9	0
10	...	6
11	74
28	0
29	267
Sept. 9	...	2
11	9	...
12	12	...
14	5
15	39
16	2
19	0
20	...	9
23	109
Geometric mean catch	142	5	0	0	15	13
95% confidence range	73-279	2-12			7-31	4-47
Mean catch date	Aug. 9	Aug. 12			Aug. 12	Aug. 19

This table also lists (the appropriate) geometric mean catches per unit effort, 95% confidence ranges and mean dates, the calculations of which are set forth in Appendix I.

TABLE IV. Estimates of density and total number of fingerling sockeye salmon in the Babine-Nilkitkwa nursery area: August 9-19, 1956.

Region	Fingerling sockeye salmon	
	Number acre	Total number
		<i>millions</i>
North of Halifax Narrows:		
Nilkitkwa Lake	1420	1.7
North Arm: outlet to 9 Mile Point	50	0.3
North Arm: Sunnyside to Halifax Narrows	0	
Subtotal		2.0
South of Halifax Narrows:		
Old Fort to Bear Island	0	
Central Babine—Red Bluff to Black Point	150	6.9
Southern Babine—Black Point to south end	130	3.6
Subtotal:		10.5
Total:		12.5

DENSITY AND DISTRIBUTION

Table IV is presented using 10 as the factor for converting geometric mean tow-net catch to fish per acre. Of the estimated 10.5 million fingerlings south of Halifax Narrows, approximately 70% or 7.4 million are indicated as progeny of kokanee (Appendix II). This leaves the following estimated numbers of anadromous fingerlings:

North of Halifax Narrows	2.0
South of Halifax Narrows	3.1
Total	5.1

Although no precision is claimed for the separation of fingerlings as to parentage, it is noteworthy that the estimated numbers of anadromous fingerlings north and south of Halifax Narrows is approximately in the same ratio as the number of parent anadromous sockeye: 19,160 north of Halifax Narrows and 27,800 south. Also, the potential egg deposition of kokanee which spawned south of Halifax Narrows in 1955 was more than twice that of the anadromous sockeye spawning there.

During 1956, no fingerling sockeye were caught in the entire region of Babine Lake between Sunnyside, at the midpoint of the North Arm, and Bear Island in the main part of the lake. This region has only one spawning tributary—the Morrison River—which had only an estimated 1,800 spawners in 1955 (Table I). This indication of extremely low density of fingerlings in this region again points to limited dispersal in the lake away from the place where they entered as fry.

DISPERSAL VS. POPULATION DENSITY

The 1956 catches suggest less dispersal of fish from the Babine River spawning grounds than in 1955. In 1956, Nilkitkwa Lake had 85% of the two million

fingerlings estimated to be north of Halifax Narrows, and few, if any, had dispersed farther south than 9 Mile Point. Even of the 15% in the North Arm, a certain small number would be from spawning on 5 Mile and 9 Mile Creeks rather than the Babine River. In 1955, with a much larger population, Nilkitkwa Lake had only 10% to 15% of the estimated 38 to 53 million fingerlings north of Halifax Narrows. Also, in 1955 considerable numbers of fish were found south of 9 Mile Point. These distributions indicate greater population dispersal associated with high population density.

GROWTH

The fingerling sockeye of Nilkitkwa Lake appear to have attained a mean weight of approximately 4 grams by mid-October, 1956: the sample of 109 taken on September 23 had a mean weight of 3.76 grams, with a 95% confidence range of 3.56–3.96 grams. Samples from the North Arm were too small for a precise description of size, although a mean weight of 4.4 grams for 3 fingerlings taken on November 9 suggests a comparable rate of growth. Such higher rates of growth in 1956 at lower population densities supports the view that the extremely slow rates of growth in these regions in 1955 were a result of crowding. In regions south of Halifax Narrows samples were also insufficient for any precise estimation of size attained by mid-October, but a mean weight of 4.5 grams for a sample of 6 fingerlings taken on October 27 suggests a rate of growth comparable to that of the other regions in 1956.

FURTHER EVIDENCE CONCERNING THE DENSITY OF 1956 FINGERLINGS

The total seaward migration of yearling sockeye in May and June, 1957, was estimated as 6 to 7 million. This figure is certainly within the range of numbers that could be expected from an estimated 12.5 million fingerlings in August, 1956 (Table IV). Samples from this smolt migration had a mean weight of 5.8 grams. Unlike 1956, there were no distinguishably different size groups.

Tow-net catches of yearling sockeye throughout the lake area in 1957 declined as the seaward migration progressed. After this emigration yearlings were taken only very rarely north of Halifax Narrows; but in regions south of this narrows 1 or 2 yearlings per standard tow were taken rather consistently. If catchability of yearlings is comparable to that of fingerlings, these catches would suggest a population of the order of 1 to 2 million yearlings remaining south of Halifax Narrows in 1957. These yearlings would presumably be progeny of kokanee, but at this rate they were much less numerous than the yearlings which migrated seaward, and much less numerous than the 1956 fingerling estimates indicated. This discrepancy could mean either that yearling kokanee are less catchable than fingerlings, or that a majority of the kokanee progeny went to sea, or that the separation of kokanee from anadromous fingerlings was faulty, or perhaps that the estimate of the seaward migration was in error, or some combination of these. They may even migrate as 2-year-old smolts in 1958, though such smolts have previously always been very scarce at Babine.

THE FINGERLING SOCKEYE OF 1957

During the 1957 field season, tow-net sampling was carried out in 9 regions, which are more or less discrete basins (Fig. 1):

- (1) lower Nilkitkwa Lake;
- (2) upper Nilkitkwa Lake;
- (3) the North Arm between the outlet and 9 Mile Point;
- (4) the North Arm between 9 Mile Point and Sockeye Point;
- (5) the North Arm between Sockeye Point and Halifax Narrows;
- (6) between Old Fort and Bear Island;
- (7) in Morrison Arm;
- (8) central Babine—between Red Bluff and Black Point;
- (9) southern Babine—between Black Point and the south end of the lake.

No sampling was done in Hagan Arm but it is likely that the numbers of fingerlings there were negligible.

A few fingerling sockeye were taken by tow-netting in early June, but, as in 1956, it appeared that it was late June before all of the fry had entered the lake area and taken up their pelagial residence. Visual observations of masses of fry moving from the Upper Babine River and along shore for a short distance into the North Arm indicated the peak of the fry movement into this lake region occurred during the period of June 15 to 25.

Table V presents the 1957 catches of fingerling sockeye per unit of effort made during the period from June 30 up to the time in October when surface water temperatures had fallen below 7°C. and after which catchability was greatly reduced.

TABLE V. Catch per standard unit of effort of fingerling sockeye salmon, 1957.

Date 1957	Lower Nilkitkwa Lake	Upper Nilkitkwa Lake	Outlet to 9 Mile Pt.	9 Mile Pt. to Sockeye Pt.	Sockeye Pt. to Halifax Narrows	Old Fort to Bear Is.	Morrison Arm	Central Babine	Southern Babine
June 30	1606	868
July 3	32
4	186
5	623
6	2
7	14
9	...	1569
11	292
12	117
15	59
16	102
17	51
21	16
22	251
23	643
24	36
25	9	...	99	...
26	44	...
27	29	...
28	383
29	258	174
31	49

Date 1957	Lower Nilkitkwa Lake	Upper Nilkitkwa Lake	Outlet to 9 Mile Pt.	9 Mile Pt. to Sockeye Pt.	Sockeye Pt. to Halifax Narrows	Old Fort to Bear Is.	Morrison Arm	Central Babine	Southern Babine
Aug. 2	17
3	39
4	148
5	105
7	181
8	436	55
9	...	791	146
10	459	238
11	543	...	20	83
15	106	...
16	69	...
17	84	...
18	134	...
19	...	481
20	810
21	389
22	272	37
23	74
26	197
30	...	340
31	458
Sept. 1	599
2	119
3	306
4	13
9	325
10	...	327
11	156
19	...	349
21	204
22	97
28	27
29	29
30	9
Oct. 2	527
3	...	790
8	133
14	187
15	...	403
16	93	...	16
17	159
24	28
29	45	...
30	139	...
31	83
Geometric mean catch	486	575	272	205	26	5	15	62	102
95% con- fidence range	321-736	405-807	169-439	146-289	17-41	40-97	68-154
Mean catch date	Aug. 25	Aug. 26	Aug. 22	Aug. 22	Aug. 21	July 15	July 20	Sept. 1	Aug. 7

DENSITY AND DISTRIBUTION

Conversion of mean catch per unit effort data to estimates of population density, expressed as fish per acre, is made as for the 1956 data using the factor 10.

On this basis Table VI lists estimates of density and total population in each of the areas sampled. These estimates are for the period August 21-25, 1957: that is, mean catches for the regions south of Halifax Narrows have been adjusted to August 23 assuming a mortality rate comparable to that demonstrated by Foerster (1938) and indicated in regions north of Halifax Narrows (Appendix I).

TABLE VI. Estimates of density and total number of fingerling sockeye salmon in the Babine-Nilkitkwa nursery area: August 21-25, 1957.

Region	Fingerling sockeye salmon	
	Number per acre	Total number <i>millions</i>
North of Halifax Narrows:		
Lower Nilkitkwa Lake	4860	2.9
Upper Nilkitkwa Lake	5750	3.5
North Arm: outlet to 9 Mile Point	2720	13.6
North Arm: 9 Mile Point to Sockeye Point	2050	5.7
North Arm: Sockeye Point to Halifax Narrows	260	0.8
Subtotal:		26.5
South of Halifax Narrows:		
Old Fort to Bear Island	30	0.4
Morrison Arm	130	0.5
Central Babine—Red Bluff to Black Point	680	31.3
Southern Babine—Black Point to south end	890	24.9
Subtotal:		57.1
Total		83.6

Of the estimated 57.1 million south of Halifax Narrows, 39% or 22.3 million are believed to have been progeny of kokanee (Appendix II). This leaves the following estimated numbers of fingerlings believed progeny of anadromous sockeye:

North of Halifax Narrows	26.5 million
South of Halifax Narrows	34.8 million
Total	61.3

Although no great precision is claimed for the separation of anadromous sockeye and kokanee, the larger number and size of the samples make it more reliable than in 1956. As in 1956, the estimated number of fingerling progeny of anadromous sockeye north and south of Halifax Narrows (26.5 and 34.8 million, respectively) stands in a ratio similar to that of the estimated number of parent anadromous spawners (119,500 north and 148,850 south of Halifax Narrows). Also, the egg potential of kokanee spawning in 1956 suggests that about 35% of the fingerlings south of Halifax Narrows in 1957 could be progeny of kokanee—in good agreement with the 39% estimated.

In 1957, as in 1956, the lowest densities of fingerlings were found in the regions between Sockeye Point and Bear Island, again indicating limited dispersal of these fish in the lake from their points of origin. The findings throughout give conclusive evidence of the dependence of fingerling distribution on the

distribution of parent spawners to the tributary spawning grounds, and of more or less limited dispersal from such points of origin. As pointed out earlier (Johnson, 1956) the limited dispersal appears to be a function of the multibasin nature of this lake system; the dynamics of such dispersal will be dealt with in another paper.

DISPERSAL VS. POPULATION DENSITY

The 1957 dispersal from the Babine River spawning grounds, as indicated by Tables II, IV, VI and VII, appears intermediate between that of 1955 and 1956. (The progeny of the insignificant number of spawners in 5 Mile and 9 Mile Creeks are considered negligible in this comparison, see Table I.) Although only three points of comparisons are available here, a direct relationship between extent of dispersal and population density is clearly suggested. General ecological significance for such a relationship has been suggested by Allee *et al.* (1949), based on the findings of Crombie (1944) with experimental insect populations and Errington (1939) with muskrat populations.

TABLE VII. Dispersal of fingerlings resulting from Babine River spawning, as measured by the percentage remaining in Nilkitkwa Lake, of the total fingerlings north of Halifax Narrows.

Year	Estimated fingerlings in Nilkitkwa Lake	Estimated sockeye spawning in the Babine River the previous year
1955	10% to 15%	255,000
1956	85%	19,000
1957	24%	119,500

In the case at hand, it is doubtful that any conceivable level of density would serve to disperse any significant portion of fingerling sockeye, progeny of Babine River spawners, farther up-lake (south) than the Halifax Narrows region. For, even with the extremely high fingerling densities of 1955, high levels of zooplankton abundance in the Halifax Narrows region in August suggested relatively low densities of fingerling sockeye there.

GROWTH

The higher density of fingerling sockeye in 1957, coupled with a much more intensive sampling program, resulted in much more detailed information on growth than was obtained in the two previous years. The ecology of these growth rates will be dealt with in detail elsewhere (Johnson, MS), but certain features are pertinent to this discussion.

For the five regions (north of Halifax Narrows) which were most intensively sampled, the fingerling sockeye attained approximately the following mean weights by mid-October, 1957:

Region	Mean weight in grams
(1) lower Nilkitkwa Lake	2.2
(2) upper Nilkitkwa Lake	1.8
(3) North Arm: Outlet to 9 Mile Pt.	3.6
(4) North Arm: 9 Mile Pt. to Sockeye Pt.	3.7
(5) North Arm: Sockeye Pt. to Halifax Narrows	5.7

The differences are significant in all cases except that between regions (3) and (4), and in this case the difference in size was significant throughout the period July–September, 1957. These differences in growth are taken as evidence that these five more or less distinct basins did have quite discrete fingerling sockeye populations during the 1957 period of study; and they imply that there is relatively little movement from one basin to another once lake residence is established.

The much less intensive sampling in regions south of Halifax Narrows in 1957 did not yield a detailed picture of growth such as was obtained for regions north; and results are further complicated by the indication that the fingerlings south of Halifax Narrows were a mixture of anadromous and smaller kokanee progeny. However, these fish attained a mean weight of 4 to 4.5 grams by mid-October, 1957, suggesting that the larger group (believed progeny of anadromous sockeye) had probably attained a weight of roughly 5 grams; that is, their growth was most comparable to that of the sockeye in southernmost region of the North Arm.

By comparison, the approximate sizes of fingerlings in mid-October in the previous two years (see above) were indicated as follows:

Region	Mean weight in grams	
	1955	1956
Nilkitkwa	1.1	4
North Arm: north half	1.4	(4)
North Arm: south half	1.7	no samples
South of Halifax Narrows	(3.4)	(4)

The mean weights shown in parentheses were derived from extremely small samples and little can be said for them other than that they give a gross indication of relatively high growth rates, not significantly different from those in Babine Lake in 1957.

The very low growth rate of fingerlings in Nilkitkwa Lake in 1957, as compared to 1956, at high population densities again indicates that crowding retards growth (see also, Johnson, MS). The rate of growth in Nilkitkwa Lake in 1957, higher than in either Nilkitkwa Lake or the North Arm in 1955, suggests that population densities in these regions in 1955 might have been higher than in Nilkitkwa Lake in 1957—rather than lower as indicated by the tow-net estimates (Tables II and VI). In view of the rather inadequate data on which the 1955 tow-net estimates were based, this evidence from growth may actually be a more reliable indication of density in 1955.

SUMMARY AND CONCLUSIONS

Table VIII, although inadequate in itself and subject to limitations of the methods as discussed throughout, summarizes the estimates of the fingerling populations and the related parent populations. Further breakdown by regions is given in Tables I, II, IV and VI.

TABLE VIII. Summary of estimates of the fingerling sockeye populations of 1955, 1956 and 1957, and the spawning parent populations in the Babine-Nilkitkwa Lakes nursery area. Kokanee estimates are in terms of equivalent numbers of anadromous sockeye (see Appendix II).

	Spawning sockeye populations		Fingerling sockeye populations	
	Anadromous	Kokanee	Progeny of anadromous	Progeny of kokanee
			<i>millions</i>	<i>millions</i>
North of Halifax Narrows South of Halifax Narrows Totals	1954	few few few	1955 (August-October) 38.2 to 52.9 7.1 to 19.3 45.3 to 72.2	no estimate but apparently insignificant
North of Halifax Narrows South of Halifax Narrows Totals	1955	few 62,000 62,000	1956 (August 9-19) 2.0 3.1 5.1	insignificant 7.4 7.4
North of Halifax Narrows South of Halifax Narrows Totals	1956	few 81,000 81,000	1957 (August 21-25) 26.5 34.8 61.3	insignificant 22.3 22.3

Analysis of variation in catch per unit effort with tow-net gear, and the generally logical development of the findings, indicate that the catch per unit effort method of population estimate employed is basically sound.

Density and distribution of fingerling sockeye salmon throughout this lake area is related to, and concluded to be dependent on, the density and distribution of the parent spawners on the tributary spawning grounds.

Discrete populations of fingerlings in more or less discrete basins suggest a limited dispersal which is a function of the multibasin nature of this lake system.

Larger populations appear to disperse a greater distance and in relatively greater numbers into the North Arm of Babine Lake (Table VII).

When present in sufficient numbers, the freshwater-maturing sockeye (here called kokanee) appear to contribute significantly to the fingerling populations south of Halifax Narrows, but it is not yet known whether or not they may contribute to, or be partly derived from, the anadromous stock.

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APPENDIX I. ANALYSIS OF VARIATION IN CATCH PER UNIT EFFORT BY TOW NETS

The series of collections made over the relatively short period of August 3 to 8, 1957, in the southern part of Babine Lake (Table V) were made for the purpose of examining variation in catch per unit of towing effort. It is likely that there was no appreciable change in population size during this short period. This series of 9 catches per unit effort yielded the following skewed array:

39, 55, 83, 105, 146, 148, 181, 238, 332

To obtain a more symmetrical distribution a transformation to logarithms was made:

1.59, 1.74, 1.92, 2.02, 2.16, 2.17, 2.26, 2.38, 2.52

Statistics calculated are:

Mean = \bar{x} = 2.08; antilog = 120

Standard deviation = s = 0.2990

95% confidence limits = 1.85 and 2.31; antilogs = 71 and 204

As an expression of variation in terms of the geometric mean (120), the 95% confidence range (204 - 71 = 133) is 111% of this mean.

Further evaluations of the variation in catch per unit effort can be had from a series of regressions of log catch on time, using the data of Tables III and V, assuming constant catchability and a constant mortality rate during the times involved. Logarithmic transformation of catch data is used throughout because of obvious skewness and an approximate proportional relation between mean and standard deviation (evidenced by range). Table A presents a summary of such regression analyses of logarithm of catch per unit effort on time; the unit of time is one day. The standard deviation measured from the regression line, s_{yx} , is a statistic comparable to the standard deviation calculated for the 9 catches above.

Except for the one series (south Babine, 1956) with s_{yx} = 0.4761 and believed a result of aberrant sampling, the standard deviations from regression range from 0.1946 to 0.2897 and compare favorably with the standard deviation of 0.2990 of the series of 9 catches above. The only other comparable series of catches available (from Lakelse Lake in 1955) shows a standard deviation from regression of 0.3100. Such relatively uniform values of standard deviation for all these differing regions indicate a rather standard variability in catch per unit effort.

It is interesting to note that the smallest standard deviations are for catches from upper and lower Nilkitkwa Lake. This may be related to the fact that these two basins are much the smallest of those with which we are here concerned; that is, one standard unit of fishing effort with this gear may sample smaller basins more efficiently than larger basins.

Table A also gives the appropriate means (geometric) of catches used throughout this paper and their confidence limits. As a means of expressing variation (relative accuracy) in original catch terms, the confidence range in each case has been expressed in terms of percentage of the geometric mean. Regarding the accuracy of such catch per unit effort data as an indication of population density, it appears that (if our assumption of constant catchability and mortality holds true) the geometric mean of the catches has a 95% confidence range of the order of 70% to 99% of its value. The nature of this tow-net fishing effort is such that it would in most cases be impossible to exert enough units of effort to appreciably reduce the confidence range. Nine to 12 tows per basin per season appears to be a reasonable order of sampling intensity. One or two tows (as in 1955) can give a gross indication of density—which for some purposes is sufficient.

Table A also gives the regression coefficients. Although there is no significant difference between any of these, there is best agreement among those for the five 1957 sampling regions in which sampling was well spaced throughout the period of study. These range from -0.0042 to -0.0058, their antilogarithms corresponding to survival rates of 25% to 38%; thus

indicating mortality for the 100 day period, June 30 to October 8, of 64% to 75%. Computation of a mortality rate of course implies that it is constant throughout this period, and also that catchability is constant. The only direct evidence in support of these assumptions is the general regularity of the decrease in catch, and the similarity of rate of decrease, in these different basins: the lines of Fig. A do not have any consistent suggestion of curvature in one direction or the other. Of course, it is conceivable that a seasonal trend in mortality rate might be cancelled by an opposite trend in catchability. It is pertinent that a mortality rate of this same order, for fingerling sockeye during this period of their life, was estimated by a completely different method at Cultus Lake (Foerster, 1938).

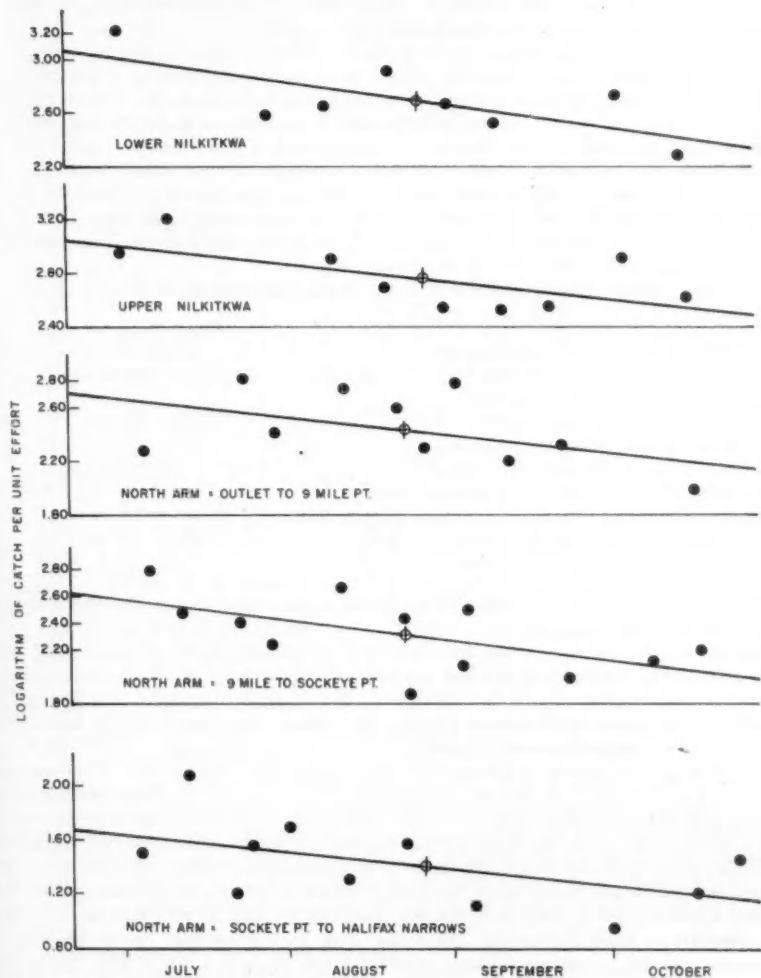


FIG. A. Regressions of logarithm of catch per unit effort on time, showing the mean point on each regression line.

APPENDIX II. THE FRESHWATER TYPE OF SOCKEYE SALMON IN THE BABINE-NILKITKWA NURSERY AREA.

The name "kokanee" is used in this paper for the freshwater-maturing type or types of sockeye salmon in the Babine-Nilkitkwa area. Strictly defined, "kokanee" applies to populations of *O. nerka* that are self-contained and independent of sea-run sockeye, even where the latter occur in the same habitat. The Babine kokanee have not yet been intensively studied, and it is possible that some of them are progeny of the anadromous sockeye—the "residual" sockeye of Ricker (1938). It is also possible that some of the progeny of the non-anadromous fish may go to sea and so contribute to the anadromous stock. The information summarized below is from incidental collections and observations made by Fisheries Research Board personnel and by Fisheries Officer L. J. Gelley.

Among Babine kokanee there appears to be a consistent predominance of males in the spawning population³ (about 75%); the time of onset of spawning is earlier than for anadromous sockeye on the same grounds, but broadly overlaps that of the anadromous form. The color of males at maturity is the same as that of anadromous sockeye. Most specimens examined were maturing in the 4th year of life; however a few 3-year-old and 5-year-old spawners have also been noted. Mean fork length at maturity is about 10 inches. Egg counts for 12 female kokanee in 1953 showed a mean of 390 eggs per female, compared to a mean of 3300 eggs per female anadromous sockeye shown by samples from this area. That is, egg content of kokanee females is roughly $\frac{1}{8}$ of that of the anadromous females. The diameter of the kokanee eggs is about $\frac{1}{2}$ of that of anadromous eggs.

Mr. Gelley lists the Babine-Nilkitkwa kokanee spawning grounds as follows (see Fig. 1 and Table 1):

- Tachek Creek—principal spawning ground
- Grizzly Creek (branch of Beaver River)—important, but secondary to Tachek Creek
- Twin Creek—moderately important
- Pierre Creek—moderately important
- Pendleton Creek—moderately important
- 4 Mile Creek—a few hundred spawners at most
- 6 Mile Creek—a few hundred spawners at most
- Sockeye Creek—a few hundred spawners at most
- 9 Mile Creek—a few hundred spawners at most
- 5 Mile Creek—a few hundred spawners at most

Occasionally a few kokanee are observed to spawn in the other streams. In addition, some spawning in the lake is suspected.

There are only two very minor kokanee spawning grounds north of Halifax Narrows—9 Mile and 5 Mile Creeks. Also, gill net and tow net catches of yearling and older sockeye in the various lake regions suggest that kokanee are found primarily south of Halifax Narrows. On this basis, it seems unlikely that progeny of kokanee contributed significantly to the fingerling sockeye populations north of Halifax Narrows in any of the years 1955–1957.

The abundance of spawning kokanee in 1954 was less than average and, considering the large number of anadromous spawners, was probably inadequate to contribute significantly to fingerling populations south of Halifax Narrows. However, an unusually great abundance of kokanee spawners in 1955, and even greater numbers in 1956, make it possible that some considerable portion of the fingerlings south of the Narrows in 1956 and 1957 may have been progeny of kokanee. For example, Mr. Gelley estimated the number of kokanee spawning in Tachek Creek in 1955 as 400,000 to 500,000, and that the total for all tributaries may have been 1,000,000 or more. Assuming 75% males, and an egg content one-eighth that of anadromous sockeye, a million kokanee would be the equivalent of 62,500 anadromous sockeye with a 50–50 sex ratio; that is, they would contain more than double the number of eggs in the 27,800 anadromous spawners south of Halifax Narrows in 1955. Thus, approximately 70% of the fingerling sockeye south of Halifax Narrows in 1956 may have been

progeny of kokanee. Similarly, an even greater abundance of kokanee spawners in 1956 (possibly 1.3 million) suggests that their progeny may have comprised about 35% of the fingerling population south of Halifax Narrows in 1957.

SEPARATION OF FINGERLINGS AS TO PARENTAGE: FRESHWATER OR ANADROMOUS SOCKEYE.

There is no known morphological criterion for distinguishing between fingerling sockeye of anadromous parentage and fingerling sockeye of kokanee parentage. However, the kokanee eggs are smaller and the following suggests that a size difference might be maintained for some time.

Withler and Aro (MS) studied sockeye spawning at 6 Mile Creek, Babine Lake, in 1953. They put pairs of ripe anadromous sockeye and kokanee simultaneously into different pens embedded in the creek bed, in which spawning then took place. On their emergence in the spring of 1954, the resulting fry were significantly different in size: the fry from anadromous sockeye had a mean fork length of 27.5 mm. (range: 26 to 29), and the fry from kokanee had a mean fork length of 23.1 mm. (range: 22 to 27).

Vernon (1957, p. 591) presents evidence that such a size difference in newly hatched fry would be reflected in growth rate during at least the following six months. He took kokanee of three different races, spawned them artificially and maintained the progeny of a common environment (three parallel hatchery troughs with a common water source) from fertilization to six months after hatching. The mean fork lengths were as follows:

	2 weeks after hatching	6 months after hatching
Group 1	21.4 mm.	36.6 mm.
Group 2	22.4 mm.	41.1 mm.
Group 3	22.6 mm.	41.3 mm.

The difference in length between group 1 fish and group 2 or group 3 fish was significant at both times.

Although length frequency distributions of samples of fingerlings from Babine and Nilkitkwa exhibited no obvious bimodality, the existence of broadly overlapping size groups was considered possible. To investigate this possibility, probability graph paper was employed according to the method of Harding (1949). In this method, when any normally distributed population is plotted in the prescribed manner, the points all fall on a straight line: the position of the line being determined by the mean and its slope by the standard deviation. When a bimodal or polymodal distribution, of compounded normal distributions, is plotted it gives a curve which is the resultant of two or more straight lines which give the means and standard deviations of the component populations. When the component populations overlap greatly, no precise analysis can be expected; however, their existence can at least be indicated.

The length frequency of nearly all fingerling samples of sufficient size taken in 1956 and 1957 were analyzed by this method; 2-mm. length intervals being used.

1956 SAMPLES: of 4 samples from Nilkitkwa Lake, 3 gave straight-line plots typical of a single normally distributed population. The other sample neither gave a straight line nor did it indicate polymodality, suggesting an aberrant sample. For all 3 of the samples of sufficient size from south of Halifax Narrows the plots suggested bimodality but with a high degree of overlapping of the two component length groups. The indicated percentage of fingerlings in each sample constituted by the group of smaller fish is given in Table B.

1957 SAMPLES: of 37 samples from north of Halifax Narrows, 30 gave the straight-line plots indicating single normally distributed populations. Of 13 samples from lake regions south of Halifax Narrows, 10 seemed bimodal with a high degree of overlap. The percentages of smaller fingerlings in these 10 samples are shown in Table B.

TABLE B. Percentage of fingerlings in samples from south of Halifax Narrows constituted by the smaller of two length groups. Based on probability graph paper plots.

1956 samples	1957 samples
55%	50%
55%	35%
25%	30%
	45%
Mean: 45%	35%
	75%
	20%
	30%
	45%
	30%
	Mean: 39%

In either year, the smaller of the two size groups in regions south of Halifax Narrows can plausibly be considered the progeny of kokanee. The rather large number of samples available in 1957 permits some confidence in the estimate of 39% kokanee that year. It also agrees well with the figure 35% which represents the estimated contribution of kokanee to the total egg deposition of the parent populations. The 1956 estimate of 45%, based on only 3 samples, is much less reliable; but, considering the variability shown in Table B, it is not inconsistent with the estimate of 70% based on relative egg potential of the parent populations.

Summarizing, the fingerling sockeye north of Halifax Narrows, both in 1956 and 1957, appear to be almost exclusively progeny of anadromous sockeye. South of Halifax Narrows a considerable portion, in both years, appear to be progeny of kokanee. The best estimates of this kokanee portion are 39% in 1957 (from the fingerling samples themselves) and about 70% in 1956 (based on the abundance of the two types of spawners in 1955). These estimates are used above for all regions south of Halifax Narrows.

The Occurrence of Juvenile *Corynosoma* (Acanthocephala) in Pacific Salmon (*Oncorhynchus* spp.)¹

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ABSTRACT

Of 2406 *Oncorhynchus nerka* and *O. gorbuscha* collected in 1955 and 1956 from many localities throughout their range in the North Pacific and adjacent seas, 1.79% were infected with juvenile Acanthocephala of the genus *Corynosoma*. In *O. nerka* the genus was represented by *C. strumosum*, *C. villosum*, *C. semerme* and *C. hadweni*, all of which use Pinnipedia as the normal definitive hosts. *C. strumosum* and *C. villosum* were found in *O. gorbuscha*. Apparently there are no previous reports of the genus *Corynosoma* in *Oncorhynchus*, nor of *C. semerme* and *C. hadweni* in any intermediate host in the North Pacific region. *O. nerka* is the first recorded intermediate host of *C. villosum*. Data on incidence and intensity of infection of the two hosts by each of the species and the locality and date of catch of the infected salmon are tabulated. Brief descriptions of the four species, based on the collected specimens, are given.

INTRODUCTION

THE GENUS *Corynosoma* Lühe, 1904 (Acanthocephala: Palaeacanthocephala: Polymorphidae) utilizes birds and mammals associated with an aquatic environment as definitive hosts. The marine species of *Corynosoma* are largely normal parasites of Pinnipedia and to a lesser extent birds, Cetacea, and one species of Fissipedia (*Enhydra lutris*, the sea otter). For marine species, where known, the intermediate hosts include a crustacean as the first host and a fish as the second host. In fish the juvenile parasites are located in cysts attached to mesenteries or visceral organs.

Within the range of salmon (*Oncorhynchus* spp.) distribution in the North Pacific region (including the Bering and Okhotsk Seas) 6 species of *Corynosoma* have been recorded from Pinnipedia, one from a whale, *Physeter catadon*, and one from the sea otter (Van Cleave, 1953; Margolis, 1954, 1956; Krotov and Delyamure, 1952; Delyamure, 1955; Afanasev, 1941). Two of the species found in Pinnipedia have been reported also from the sea otter. In this same area, fish intermediate hosts are known for only one² of these species, namely *Corynosoma strumosum* (Van Cleave, 1953; Margolis, 1956). Since little information is available on the fish intermediate hosts of *Corynosoma* in the North Pacific region, the present account of the occurrence of 4 species in 1 genus of fishes is of interest.

The 4 species, *C. strumosum* (Rudolphi, 1802), *C. semerme* (Forssell, 1904), *C. villosum* Van Cleave, 1953 and *C. hadweni* Van Cleave, 1953 (? = *C. wegneri* Heinze, 1934), were found in sockeye salmon [*Oncorhynchus nerka* (Walbaum)], and *C. strumosum* and *C. villosum* in pink salmon [*Oncorhynchus gorbuscha*

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²Schiller (1954) reported larval *Corynosoma* from *Lebius superciliosus* and *Hemilepidotus hemilepidotus* taken at Amchitka Island, Alaska, but the species was not identified.

(Walbaum)] during a general study of the parasites of these fish. In addition to representing the first account of *C. villosum* in an intermediate host, these findings also record new intermediate hosts for the other 3 species. Fish intermediate hosts for *C. semerme* and *C. hadweni* have not been reported previously in the North Pacific region.

COLLECTION AND PREPARATION OF SPECIMENS

The salmon examined were collected between May and October in 1955 and 1956 from many localities throughout their range in the North Pacific and adjacent seas. These included samples from the Okhotsk Sea and Hokkaido, Japan, across the North Pacific and Bering Sea to North America from Alaska to the Columbia River. Collections of the salmon were achieved through the co-operation of Japanese, United States and Canadian agencies as part of the research program of the International North Pacific Fisheries Commission. All fish were frozen immediately after capture and subsequently shipped to Nanaimo, where they were thawed and examined.

Most *Corynosoma* specimens, upon recovery, after washing in fresh water, had the proboscis completely or partially withdrawn. Initially no attempt was made to extrude the proboscis before fixation. After collection of about 15 specimens, it was discovered that slight pressure applied to the bulbous portion of the body with the flat edge of a curved dissecting needle often brought about extrusion of the proboscis and the posterior extremity. Excessive pressure ruptures the fore-trunk without eversion of the proboscis. Placing the specimen in a solution of 0.5% trisodium phosphate has been found to be a valuable aid in extending the body and bringing about extrusion of the proboscis. In this solution specimens become turgid, unless the cuticle has been previously ruptured, facilitating the eversion of the proboscis under slight external pressure; and some specimens have been observed to evert the proboscis spontaneously in a few hours. In other specimens, even after trisodium phosphate treatment, the proboscis has remained withdrawn. In these specimens compression between a slide and coverslip was necessary to force extrusion of the proboscis. Specimens treated in this manner are, of course, flattened. If, however, the specimen has been treated previously with trisodium phosphate and after compression it is returned to this solution before fixation, the original plump shape of the body and proboscis can be restored.

Although at the present time it appears that extrusion of the proboscis can be brought about in almost all specimens of *Corynosoma* recovered from frozen salmon, a number of specimens collected early in this study were fixed with the proboscis and posterior extremity entirely or partially introverted. Most specimens in which the proboscis was not everted were dissected for identification. In dissected specimens it was often difficult to obtain an exact count of the number of longitudinal rows of proboscis hooks and with these specimens identifications were based on the number of small and large hooks in each row, the size of the heaviest of the large hooks, the size of the genital spines, the distribution of body spines and the general body shape. Some specimens, in which only the anterior

portion of the proboscis remained introverted, were not dissected. In these specimens, the number of longitudinal rows of hooks could be determined from whole mounts but the total number of hooks in each row could not be determined with certainty. Identifications were based on the number of rows of hooks, the number of small hooks in each row, the size of the heaviest hooks, the distribution and size of genital spines and general body shape.

Whole specimens were stained in Grenacher's borax carmine and mounted in Canada Balsam.

Generally, the descriptions of species provided by Van Cleave (1953) were used as a basis for identifications. Van Cleave's studies on *Corynosoma* were largely centered about collections from marine mammals of the Alaska region.

INCIDENCE

The incidence of *Corynosoma* spp. in the sockeye and pink salmon samples collected in 1955 and 1956 is shown in Table I. Less than 2% of 2,406 salmon were infected. The incidence in the two hosts combined was somewhat greater in 1955 than 1956. In the 1956 sockeye salmon samples the incidence was a little higher

TABLE I. Incidence of *Corynosoma* spp. in sockeye and pink salmon in 1955 and 1956 samples.

Host and year	Number examined	Number and percentage infected									
		<i>C. strumosum</i>		<i>C. villosum</i>		<i>C. hadweni</i>		<i>C. semerme</i>		All species	
		No.	%	No.	%	No.	%	No.	%	No.	%
Sockeyes—1955	398	0	0.00	4	1.00	2	0.50	0	0.00	6	1.51
Sockeyes—1956	991	6	0.61	9	0.91	1	0.10	1	0.10	17	1.72
Sockeyes—1955 & 1956	1389	6	0.43	13	0.94	3	0.22	1	0.07	23	1.66
Pinks—1955	349	3	0.86	6	1.72	0	0.00	0	0.00	9	2.58
Pinks—1956	668	6	0.90	5	0.75	0	0.00	0	0.00	11	1.65
Pinks—1955 & 1956	1017	9	0.88	11	1.08	0	0.00	0	0.00	20	1.97
Pinks & sockeyes—1955	747	3	0.40	10	1.34	2	0.27	0	0.00	15	2.01
Pinks & sockeyes—1956	1659	12	0.72	14	0.84	1	0.06	1	0.06	28	1.69
Pinks & sockeyes—1955 & 1956	2406	15	0.62	24	1.00	3	0.13	1	0.04	43	1.79

than that in the 1955 samples, whereas in the 1956 pink salmon samples it was lower than in the 1955 samples. In the samples examined in 1955 the incidence in pink salmon was greater than that in sockeye salmon, but in 1956 the incidence in sockeye salmon slightly exceeded that in pink salmon.

The low incidence of juvenile *Corynosoma* spp. in the two species of *Oncorhynchus* suggests that these fish generally are unimportant in transmitting *Corynosoma* infections to pinnipeds or other definitive hosts.

Of the four species, *C. villosum* was the most common in sockeye and pink salmon, particularly in the 1955 samples. *Corynosoma strumosum* had an over-all incidence about two-thirds that of *C. villosum*. *Corynosoma hadweni* was less frequently encountered and only in sockeye salmon and *C. semerme* was the rarest species, only one specimen having been found in a sockeye salmon.

INTENSITY

The number of acanthocephalans in the infected fish varied from 1 to 5. Table II gives the number of salmon with the different levels of infection. Of the 43 infected pink and sockeye salmon, about 75% harboured only one specimen

TABLE II. Number of salmon infected with different numbers of *Corynosoma* spp. (The values in parentheses represent the percentage of the *Corynosoma*-infected hosts having the number of worms specified in the column.)

Host	No. of specimens of <i>Corynosoma</i> spp.				
	1	2	3	4	5
Sockeyes—1955	5 (83%)	0	1 (17%)	0	0
Sockeyes—1956	13 (76%)	3 (18%)	0	0	1 (6%)
Sockeyes—1955 & 1956	18 (78%)	3 (13%)	1 (4%)	0	1 (4%)
Pinks—1955	6 (67%)	2 (22%)	1 (11%)	0	0
Pinks—1956	8 (73%)	3 (27%)	0	0	0
Pinks—1955 & 1956	14 (70%)	5 (25%)	1 (5%)	0	0
Sockeyes & pinks—1955	11 (73%)	2 (13%)	2 (13%)	0	0
Sockeyes & pinks—1956	21 (75%)	6 (21%)	0	0	1 (4%)
Sockeyes & Pinks—1955 & 1956	32 (74%)	8 (19%)	2 (5%)	0	1 (2%)

of *Corynosoma*. Infections with 2 worms were four times more frequent than with 3; there were no infections with 4 worms and only one sockeye carried 5 *Corynosomas*.

DISTRIBUTION OF CORYNOSOMA-INFECTED SALMON

Table III gives the locality of capture of *Corynosoma*-infected salmon, the date of collection and the number of salmon examined, the numbers of salmon infected with each of the four species of *Corynosoma* at each locality and the number of specimens of both sexes found in each fish. In no instance was an individual salmon infected with more than one species of *Corynosoma*. Specific localities in which *Corynosoma*-infected salmon were not found are not listed in the table.

In fish as migratory as *Oncorhynchus* spp. (migrations in the neighbourhood of 1,000 miles are common occurrences and can take place within one or two months), it may be argued that locality of capture may be very distant from the locality in which the infection was acquired and hence statements on locality may be meaningless. Nevertheless the wide distribution of *C. strumosum* in *Oncorhynchus* parallels its known distribution in marine mammals of the North Pacific and adjacent seas. Moreover the distribution of *C. villosum* in *Oncorhynchus*, which was not as extensive as *C. strumosum*, is also similar to its recorded distribution in marine mammals. In mammalian hosts *C. villosum* is known from British Columbia and Alaskan waters, including the Aleutian Islands. In *Oncorhynchus*, the most westerly record was at 170°58' E. Longitude, which is close to the longitudinal meridian that passes through Attu, Aleutian

Islands. The principal definitive host of *C. villosum* appears to be *Eumetopias jubata*, Steller's sea lion. Parasitological investigations of this sea lion, as well as other Pinnipedia, in the northwest Pacific off the coast of Asia have not yielded *C. villosum* (Krotov and Delyamure, 1952). The absence of *C. villosum* from *Oncorhynchus* caught in the Western Pacific and Okhotsk Sea may thus be a direct reflection of the parasite's absence from marine mammals in that area.

TABLE III. Occurrence of three species of *Corynosoma* in sockeye and pink salmon from the North Pacific in 1955 and 1956, with the number and sex of the specimens found in each fish. A fourth species, *C. semerme*, was represented by 1 ♀ specimen in a sockeye of the 1956 Adak collection. (Where more than one fish in a sample was infected with the same species of *Corynosoma* a semicolon separates the specimens found in the individual fish.)

Locality	Date of capture	No. of fish examined	No. of fish infected with each species of <i>Corynosoma</i>		
			<i>C. strumosum</i>	<i>C. villosum</i>	<i>C. hadweni</i>
Sockeyes—1955					
Cook Inlet, Alaska	21-vii	25	1 (1♂)
Karluk, Kodiak Is., Alaska	24-viii	10	1 (1♀)
Kvichak Bay, Alaska	15-vii	10	...	1 (1) ^a	...
Attu Is., Alaska	28-vii to 9-viii	24	...	3 (1; 1; 3) ^a	...
Sockeyes—1956					
Columbia R. estuary	28-vi	25	1 (1♂)
Petersburg, Alaska	13-vii	25	...	1 (1♀)	...
Yakutat, Alaska	4-viii	25	...	1 (1♂)	...
Red R., Kodiak Is., Alaska	17-vi	25	1 (1♂)
Adak Is., Alaska	29-vii to 19-viii	23	1 (1♂, 1♀)
56° N., 165° W.	14-viii	11	...	1 (1♀)	...
51° N., 175° W.	8-viii	20	...	1 (1♂)	...
58° N., 175° W.	15-vii	13	1 (2♂)	1 (1♀)	...
51° N., 175° E.	25-viii	25	1 (1♀)
49° 35' N., 171° 46' E.	6-vii	25	1 (1♂)
51° 40' N., 170° 58' E.	15-vi	25	1 (1♂, 4♀)	4 (1♀; 1♀; 2♀; 1♀)	...
Pinks—1955					
Larsen Bay, Kodiak Is., Alaska	11-viii	13	1 (1♂)
Alitak Bay, Kodiak Is., Alaska	5,6-viii	12	...	1 (1♂)	...
Cold Bay, Alaska Peninsula	19-vii	11	...	1 (2♀)	...
Attu Is., Alaska	7 to 30-viii	25	1 (1♂, 1♀)	4 (1♀; 1♀; 1♀; 1♂, 2♀)	...
49° 48' N., 156° 50' E.	27-vii	9	1 (1♀)
Pinks—1956					
Kvichak Bay, Alaska	25-vii	12	...	1 (1♂)	...
Unalaska Is., Alaska	23-viii	24	1 (1♀)
Adak Is., Alaska	16-viii	25	2 (1♂; 1♂, 1♀)	1 (1♂)	...
Attu Is., Alaska	21-vii to 28-viii	26	1 (1♂)	3 (1♀; 1♂, 1♀; 1♂, 1♀)	...
54° N., 150° W.	17-vii	12	1 (1♀)
51° 22' N., 153° 51' E.	12-vii	25	1 (1♀)

*Specimens identified by Mr. Paul Montreuil, Institute of Parasitology, McGill University sexes not determined.

THE SPECIES OF *CORYNOSOMA* ENCOUNTERED

Corynosoma strumosum. This species was widely distributed, having been found in coastal salmon samples from the Columbia River estuary north to Kodiak Island, Alaska and west to Attu Island, and in open ocean samples within an area bounded by Longitudes 150° W. and approximately 154° E., and Latitudes 49° N. and 58° N.

Twenty-three specimens (11 ♂♂, 12 ♀♀) were collected; 12 (6 ♂♂, 6 ♀♀) from sockeye salmon and 11 (5 ♂♂, 6 ♀♀) from pink salmon.

The following brief description of the specimens includes mainly the characters on which the identifications were made. Unless otherwise noted, measurements apply to both sexes.

Body length (exclusive of neck and proboscis) 2.41 to 4.37 mm., the shorter measurements obtained from specimens with some degree of contraction of the hind-trunk, introversion of the posterior extremity or withdrawal of a portion of the fore-trunk. Minimum length of body in completely extended specimens probably about 3 mm. Swollen fore-trunk about $\frac{1}{2}$ to $\frac{1}{3}$ length of hind-trunk, but no sharp demarcation between the two. Neck 0.163 to 0.420 mm. in length. Maximum diameter of fore-trunk 0.70 to 1.18 mm.; diameter of hind-trunk 0.30 to 0.57 mm. or about $\frac{1}{2}$ to $\frac{1}{3}$ that of fore-trunk. Body spines extend ventrally only a short distance beyond the fore-trunk. Genital spines present in all males and most females; occasionally absent or only a few scattered ones in females. Maximum length of genital spines in individual specimens 25 to 35 μ . Proboscis 0.56 to 0.60 mm. in length by 0.21 to 0.28 mm. diameter at swelling, with 17 to 19 (usually 18) longitudinal rows of 9 to 11 hooks (commonly 10, less frequently 11, rarely 9). In each row 5 to 7 (commonly 5 or 6, occasionally 7) large hooks, with prominent recurved roots, from tip to swollen region and 3 to 5 (usually 4 or 5) smaller hooks, with inverted Y-shaped roots, behind these. The stem of the Y projects forward from the base of the thorn and the two arms are directed backwards. Large hooks progressively thicker posteriorly, although not necessarily longer. Frequently thorn of thickest hooks slightly shorter than more anteriorly located hooks. Thorn of heaviest hooks on proboscis swelling 60 to 70 μ long in males, 65 to 79 μ long in females.

Corynosoma villosum. This species was not as extensively distributed as the preceding one. Its southernmost coastal distribution was Petersburg, southeast Alaska. In the open ocean infected salmon were taken between 165° W. Longitude and approximately 171° E. Longitude at latitudes from 51° N. to 58° N. Thirty-two specimens (8 ♂♂, 18 ♀♀, 6 sex undetermined) were collected; 17 (3 ♂♂, 8 ♀♀, 6 sex undetermined) from sockeye salmon and 15 (5 ♂♂, 10 ♀♀) from pink salmon. In contrast to *C. strumosum*, in which the sexes were equally represented, in *C. villosum* the number of females was decidedly greater than the number of males.

Description. Trunk length 2.48 to 3.41 mm. Gradual transition from enlarged fore-trunk to hind-trunk, the former a little shorter than the latter. Diameter of fore-trunk 1.03 to 1.42 mm. and at middle of hind-trunk 0.40 to 0.58 mm. Neck 0.17 to 0.21 mm. long. Trunk spines extend ventrally the length of the fore-trunk or slightly beyond. Genital spines usually more numerous in males and absent from almost one-half of female specimens. Maximum length of genital spines in males 47 to 55 μ , in females 40 to 47 μ (sometimes only 32 or 33 μ). Proboscis 0.59 to 0.66 mm. in length by 0.25 to 0.30 mm. diameter at swollen region in males; 0.64 to 0.70 mm. by 0.25 to 0.34 mm. in females. Proboscis hooks in 22 to 27 longitudinal rows of 12 or 13 hooks of which the anterior 7 or 8 are large with prominent recurved roots and the posterior 4 or 5 (rarely 6) are small, with anteriorly directed simple roots, and

lie close together behind the swollen region of the proboscis. Thorn of anterior series of hooks increasing in thickness from tip to swelling of proboscis; length of thorn of heaviest hooks on swollen region 60 to 86 μ in male, 65 to 76 μ in female.

Van Cleave (1953) gave the number of longitudinal rows of proboscis hooks in *C. villosum* as 22 to 24, whereas there are 22 to 27 rows in the specimens from *Oncorhynchus*. The range is continuous between 22 and 27 and I have been unable to find any other characters by which the specimens with the larger numbers of rows of hooks could be distinguished from specimens with the smaller numbers. Table IV shows the number of specimens with the various numbers of rows of proboscis hooks.

TABLE IV. Frequency of various numbers of longitudinal rows of hooks on the proboscis of *Corynosoma villosum*.

		No. of longitudinal rows of proboscis hooks					
		22	23	24	25	26	27
Frequency	♂	1	2	2	1	0	0
	♀	1	1	8	1	3	2

Not included in the foregoing discussion on morphology, but listed in Table III as a male *C. villosum*, is a specimen from a pink salmon collected at Adak Island in 1956, which seems to possess all the characteristics of *C. villosum* except for 1 (or 2) fewer hooks in each longitudinal row on the proboscis. The number of hooks in each row is 11, consisting of 7 large and 4 small or 8 large and 3 small hooks. Normally in *C. villosum* the rows of hooks are comprised of 7 large and 5 small, 8 large and 4 small, 8 large and 5 small or rarely 7 large and 6 small hooks. Characters such as proboscis shape and dimensions, number of longitudinal rows of proboscis hooks (23), number of large hooks in each row, hook sizes, body shape and size of genital spines are identical with *C. villosum* and serve to distinguish the specimen from other related species. It appears that this specimen is an aberrant *C. villosum* in which 1 or 2 small hooks in each longitudinal row on the proboscis have not developed.

Corynosoma hadweni ($P=C. wegeneri$). This species was recognized in sockeyes in the Gulf of Alaska region, namely at Kodiak Island and in Cook Inlet. Three specimens (2 ♂, 1 ♀) were collected, in all of which the proboscis was completely withdrawn within the sheath and the posterior extremity was introverted. Dissection of the specimens was therefore necessary. However, even after dissection an exact count of the number of longitudinal rows of hooks on the proboscis could not be obtained.

The identification was based on the following characters. Body spines extend ventrally only a short distance beyond the fore-trunk; proboscis 0.84 to 0.86 mm. long; 9 to 11 hooks in each longitudinal row on the proboscis, of which 5 or 6 were large and 4 or 5 were small; maximum length of thickest hooks was 120 to 130 μ . The only other marine species known in the Northern Hemisphere with these proboscis characters is *C. cameroni* Van Cleave 1953, which was not reported by Van Cleave in his extensive studies of many collections of *Corynosoma* from the Alaska region. I am therefore inclined to consider the present specimens as belonging to *C. hadweni*.

In a previous note (Margolis, 1955) I suggested that *C. hadweni* was a probable synonym of *C. wegeneri*. A definite statement on this synonymy perhaps must await a re-examination of the types of *C. wegeneri*, if available, since the existing description lacks several critical details. Study of material from the type host and type locality would also prove valuable.

Corynosoma sererme. One female specimen assigned to this species was collected from a sockeye salmon taken at Adak Island, Alaska.

The proboscis of this specimen was completely introverted within the sheath and the specimen was stained and mounted without dissection. The identification as *C. sererme* was based on size and shape of the body, extent of trunk spination and size of proboscis hooks. The trunk consists of an enlarged anterior portion and a narrower posterior portion. The diameter of the hind-trunk diminishes gradually from the fore-trunk to the posterior extremity. Lengths of the hind-trunk and the fore-trunk are about equal, total trunk length being 2.38 mm. Body spines occur along the entire length of the ventral face of the trunk and are continuous with the genital spines. The genital spines have a maximum length of 46 μ . Heaviest proboscis hooks measure 72 μ long (measured from introverted proboscis).

Two other species from the North Pacific have a similar distribution of body spines: *C. validum* Van Cleave, 1953 and *C. obtuscens* Lincicome, 1943. *C. validum* occurs in pinnipeds of Alaska and geographically therefore it is available to salmon. However, it cannot be confused with the present specimen since the female is much more robust and lacks an attenuated hind-trunk. *C. obtuscens* is of the same size and general body shape as *C. sererme* but is known only from southern California and Mexico, south of the range of *Oncorhynchus* spp.

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Maximum Sustained Yields from Fluctuating Environments and Mixed Stocks¹

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ABSTRACT

Using numerical models, effects of environmental variability upon yield were tested for six single-age fish stocks characterized by different kinds and degrees of density-dependent reproduction potential. The two levels of variability examined had extremes of yield standing in the ratios 7:1 and 18:1, respectively. Close regulation of fishing to the optimum percentage for each year's stock improves the long-term average catch taken, the improvement being the greater, the more variable the environment. With the higher level of variability, improvement in average catch among five of the stocks ranged from 26% to 79% increase. However this increase in mean catch is achieved at the expense of increased variability in catch from year to year—in fact, for some kinds of stocks there must be complete cessation of fishing in some years in order to get the long-term maximum. The yield of stocks, in which reproduction *per spawner* declines at low levels of abundance, is particularly improved by a close adaptation of fishing effort to the supply of fish available.

When two or more populations of a species, characterized by different reproduction potentials, are fished in common, total potential catch is less than when each can be fished separately at its optimum level. If a common fishery cannot be avoided, the achievement of maximum average yield may find one of two originally-equal stocks as abundant or even more abundant than before the fishery began, while the other may persist only at a low level or even be exterminated completely.

INTRODUCTION

THE THEORY OF EXPLOITATION of homogeneous stocks of a fish species has had considerable attention in recent years, particularly under normal or average conditions of recruitment. This paper examines two complicating effects: (1) the influence of random environmentally-caused variability in reproduction upon the best percentage utilization of the stock, and (2) the effect of having a common fishery attack two or more stocks which differ in reproduction potential.

These two problems are examined by means of numerical models. Consideration is restricted to situations where fishing takes fish immediately prior to spawning, where there is no mixture of ages in the spawning stock, and where there is no appreciable effect of population density upon the size which the individual fish achieve at maturity. Further, the effects of population density upon survival are assumed to be some function of the number of adult spawners which produces the brood in question.

KINDS OF REPRODUCTION CURVE EXAMINED

As models of contrasting types of density effect on reproduction, six different "reproduction curves" are used (Fig. 1, 2). Curves A-C are the same as Curves

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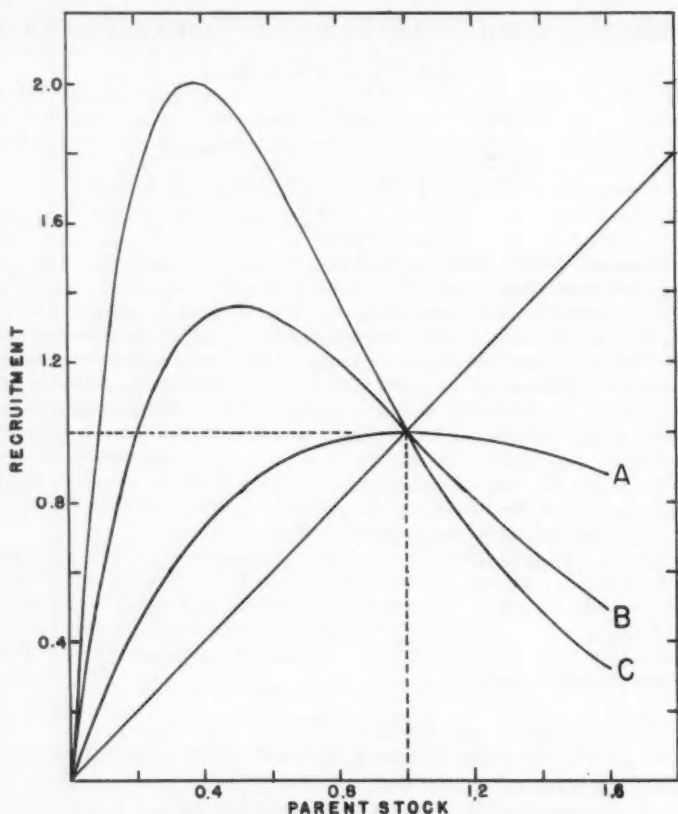


FIG. 1. Reproduction curves used (see text).

A-C of figure 11.2 of Ricker (1958). They were convenient to use because they conform to a simple mathematical expression for which numerical values had been tabulated:

$$Z = We^{a(1-W)} \quad (1)$$

Z represents the progeny and W the parental generation, both expressed as fractions or multiples of the replacement level of stock, and a is a parameter having the values 1, 2 and 2.678 respectively for Curves A, B and C. With all three curves the reproduction of the stock rises to a maximum as density of spawners increases, and then falls off; they differ in the magnitude of the maximum reproduction (relative to the replacement level) and in the size of the spawning stock which produces the maximum.

In Curve F (Fig. 2) reproduction rises rapidly to a maximum and then remains stable thereafter; the ascending limb coincides with Curve B until close

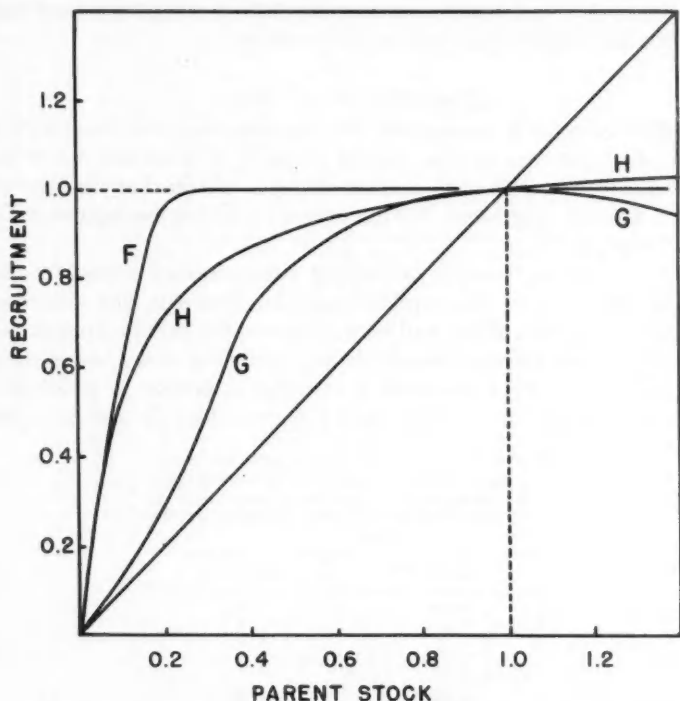


FIG. 2. Reproduction curves used (see text). Curve F coincides with B of Fig. 1, up to a point close to the level 1.0. Its lower portion is very close to Curve H, though belonging to a different family. Curve G coincides with Curve A of Fig. 1 to the right of $W = 0.4$.

to the maximum. Curve H conforms to a relationship proposed by Beverton and Holt (1957, p. 48); in order to relate it to replacement reproduction, their expression (6.10) is rewritten as:

$$Z = \frac{W}{1 + A(W-1)} \quad (2)$$

where Z and W are as above, and A is a parameter equal to the reciprocal of the maximum reproduction (when $W = \infty$). Using the value $A = 0.9$, this expression yields Curve H of Fig. 2. This particular value was selected because the resulting curve filled a gap among the other types considered: lower values of A produce curves somewhat like Curve A of Fig. 1 (to the left of the replacement point), while higher values of A give sharply bent curves, resembling F but approaching replacement reproduction gradually.

Curve G is one where the lowest stock densities are not very productive, in relation to their numbers, whereas all the other curves have the greatest production per spawner when the stock is very small. Curve G is made to coincide with

Curve A beyond $W = 0.4$, so that comparison with A will demonstrate solely the effect of the poor reproductive rate at low densities.

COMPUTATION OF YIELDS

Equilibrium catch is represented in a reproduction curve diagram, for each spawning stock density, by the vertical distance between the curve and the diagonal. Maximum equilibrium catch is obviously obtained at the level of stock where this distance is greatest. For the curves used here the figures of Table II apply.²

Effects simulating randomly-occurring environmental variability are now to be superimposed on the equilibrium-yield situations just described. An obvious model for such effects will be multipliers obtained by random selection from a table of factors whose frequencies are distributed as in a normal frequency distribution. Ricker (1954) has such a selection, a portion of which is shown here in Table I and Fig. 3B. The positive (favourable) factors are applied as

TABLE I. Sequence of randomly chosen factors used to represent the effects of environment in increasing or decreasing reproduction. Factors marked "d" are used as divisors, the others as multipliers.

"Level A"	"Level B"
2.8d	4.6d
1.5	2.0
1.2	1.4
1.1	1.2
1.2d	1.4d
1.0	1.0
2.0d	3.0d
1.1	1.2
2.3d	3.6d
1.8d	2.6d
1.1d	1.2d
1.7	2.4
1.8d	2.6d
2.5	4.0
2.0	3.0
2.0d	3.0d
2.0	3.0
2.2d	3.4d
2.2	3.4
1.3	1.6
1.4	1.8
1.2d	1.4d
2.0d	3.0d
1.7d	2.4d
1.1d	1.2d
1.5	2.0
2.2	3.4
1.6	2.2

² Because there are frequent comparisons among Tables II-IX, they are all grouped together at the end of the paper.

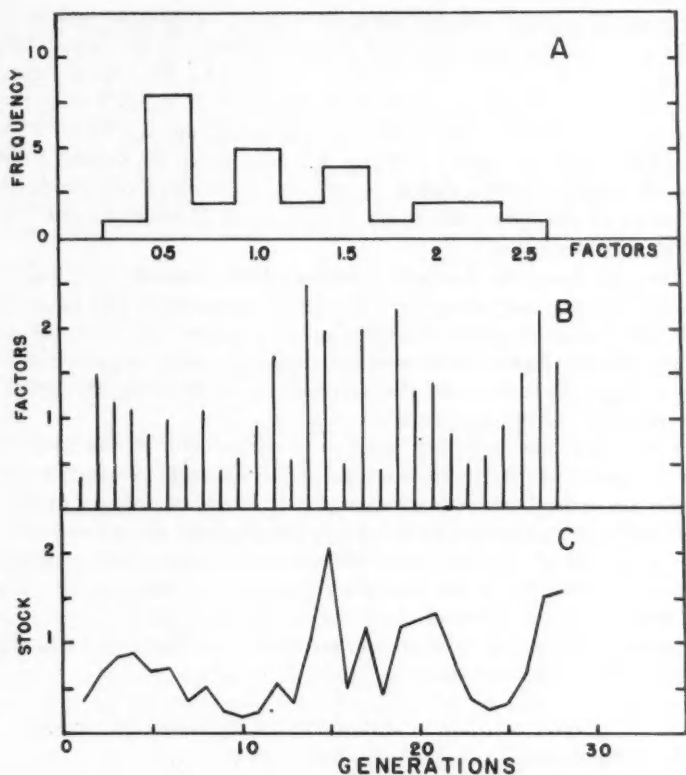


FIG. 3. A. Frequency distribution of factors representing random environmental variability at "Level A". B. The Level-A factors plotted in the order they were actually used. C. The sequence of stock sizes (before fishing) generated by Reproduction Curve A (see Fig. 1) and Level A of environmental variability.

multipliers, and the negative ones as divisors, to the mean reproduction indicated by the curve in question. This procedure produces an asymmetrical distribution of progeny sizes (Fig. 3A), which seems to accord fairly well with what is usually observed in nature among such species as pink or chum salmon—series of mediocre to moderately good years being interrupted by occasional exceptionally good ones.

The magnitude of the variability at which these factors operate can be set at any desired level. In what follows we use two different levels. In the first ("Level A"), one standard deviation is equal to unity, so that (on the average)

two-thirds of the factors³ selected for multiplication or division will lie between the limits 1 and 2, the corresponding range of effects on the population being from $\frac{1}{2}$ to 2 times the mean reproduction indicated by the reproduction curve; similarly, 19 times in 20 the range of effects lies between $\frac{1}{3}$ and 3 times the mean.

The more extreme level of random environmental effects ("Level B" has four times the variability (variance) of Level A, hence twice the standard deviation. Here, on the average, $\frac{1}{3}$ of the factors selected result in a level of reproduction that lies between $\frac{1}{3}$ of and 3 times the mean, and 19 out of 20 selections put it between $\frac{1}{5}$ of and 5 times the mean.

All tests are based on the same selection of 28 "generations" (Table I). At the "A" level the greatest multiplier is 2.5 and the greatest divisor 2.8, so that the extreme range of environmental effects is 7:1; at the "B" level the range is 18.4:1. The B-level factors were selected using the same sequence of random numbers as the A-level, in order that comparison between the two levels would indicate solely the effects of increased variability.

In every case the spawning stock was started out at the "replacement" density, designated as unity. An example of the sequence of changes in actual population size under Level A of environmental variability is shown in Fig. 3C.

Of the 28 generations in each sequence, the first four are not included in the averages to be quoted, because it was desired to allow that many generations for adjustment of the stock to the prevailing conditions of exploitation. However, their inclusion would not have changed the picture appreciably.

All stock densities, and all catches, are quoted as fractions or multiples of the replacement density of stock.

ENVIRONMENTAL VARIABILITY IN REPRODUCTION

EFFECT OF LEVEL A OF VARIABILITY UPON YIELD

What happens when random environmental variation is superimposed upon the reproduction most appropriate to each stock density? Using the smaller degree of random variability in reproduction (Level A of Table I), the arithmetic mean yield of the first five populations for 24 generations is as in Table III. (Population G is treated separately, below.)

Comparing Table III with Table II, the environmental variability evidently changes the average catch taken from Curves A, B and C very little if at all. The decrease with Population F, and the increase with H, though small, are both real.

The reason for Curve F's decreased production with environmental variability is that, operating with so high a rate of exploitation, in poor years the spawning stock is decreased to a really small size and so the next year's stock and catch are quite depressed. With Curve H the rate of exploitation is not so high and this danger is less. During good years, on the other hand, Curve H never suffers from any actual reduction in reproduction as a result of unusually numerous spawners, something which does happen with Curves A, B and C. For

³ Because the factor unity corresponds to no change, unity must be added to each deviation actually selected from the normal frequency distribution table, in which the most frequent class is of course centered at zero deviation (see Ricker, 1954, p. 572).

these reasons Population H increases its yield a little under conditions of environmental variability, even when there is no special adjustment of fishing effort to take advantage of this variability.

The most obvious effect of variable reproduction, however, is that it introduces catch differences between years. The range of year-to-year variability (ratio of greatest catch to least catch) is not very different among the five types of population, but with A and F the lowest catch is a smaller fraction of the mean, and hence would "look worse" in the statistics.

EFFECT OF PARTIAL STABILIZATION OF ESCAPEMENT

We examine next the effect of attempting to stabilize escapement in relation to a "norm"; the norm selected is the escapement which provides maximum equilibrium yield under conditions of no environmental variability⁴. These escapements are as follows (from Table II):

A - 0.433; B - 0.361; C - 0.314; F - 0.210; H - 0.240

New schedules are constructed in which rate of exploitation varies from year to year so that the above escapement norm has first priority on the stock. If less than this many fish are available, no catch is taken and the whole stock becomes escapement. If more than the norm is available, the excess is taken by the fishery but the over-all rate of exploitation does not exceed that shown in column 3 of Table II for each population. This would be a realistic picture of a fishery where it was economic to maintain sufficient gear to provide an "average" catch, but where preparation could not be made to utilize the upper extremes of population size, especially if these occurred unpredictably. The catches obtained are as in Table IV.

As compared with Table III, there is improvement in average catch from all the stocks; A is up by 9%, B by 7%, C by 8%, F by 21% and H by 5%. Except for F, however, this is accompanied by a substantial *decrease* in the size of the smallest catch taken, and for Stock A there are 5 years out of 24 when no catch at all is taken.

EFFECT OF OPTIMUM STABILIZATION OF ESCAPEMENT

With complete control of fishing and escapement, it would be possible to arrange a situation where (1) the same escapement norm is established as in the last section and this escapement has first claim on the stock; and (2) the fishery takes *all* fish above that norm, regardless of how large the stock may be. Something close to this might at times be feasible in practice, especially with valuable fish like salmon, and particularly if some fairly good prediction of the run could be made in advance.

⁴ Apparently this norm also provides the maximum sustained yield when the variable environmental factors operate. Two tests were made using Population A and Level A of environmental variability, under the conditions of Table V below, but using 0.35 and 0.50, respectively, as the norm of escapement (instead of 0.43). The mean catches were 0.45 and 0.43, both of which are less than the 0.49 obtained with the norm 0.43 described above. Similar results were obtained with Population H, using the conditions of Table III.

On the above basis, the yields for the five reproduction curves are as in Table V. This results in somewhat larger increases in average catches than the Table IV situation, though still possibly not as large as one might have expected: A is up by 36% over the Table III figure, B is up by 22%, C by 20%, F by 30% and H by 12%.

This benefit is achieved at the expense of still greater variability in catch, and this variability is greatest for Population A, where in 8 out of 24 years no catch at all was taken—all available fish were needed for escapement. For Populations C, F and H there is only a relatively small increase in variability (over Table IV), B being intermediate in this respect.

In general, we may conclude that regulation of escapements to the optimum figure for each year can improve the average take from the five populations by 12% to 36%, as compared with regulation which merely takes the best constant percentage in all years. The benefit of such regulation is greatest with populations which have a rather low reproductive potential—stock A in particular.

EFFECTS OF GREATER ENVIRONMENTAL VARIABILITY (LEVEL B OF TABLE I)

As mentioned earlier, environmental variability at Level B is 4 times as great as at Level A (log standard deviation twice as great).

Shown in Table VI is the average yield and range of yields, for the five reproduction curves, when rate of exploitation is that which would give maximum yield in the absence of environmental variation (corresponding to Table III for the lesser variability). Again there are no appreciable changes in the average catch for curves A, B and C, as compared with the conditions of no environmental variability (Table II). Population F is again a little low, while the yield of Population H is increased by 31%—the reasons were discussed on page 996. Year-to-year variation is, of course, much greater than with Level A of environmental variability.

With optimum stabilization of escapement—the fishery taking everything in excess of the spawning stocks shown in Table II—the situation is as in Table VII (corresponding to Table V for Level A of variability). The mean catch is increased: stock A is up by 79%, B by 62%, C by 55%, F by 64%, and H by 26% over the constant-exploitation situation of Table VI. These percentage increases are all much greater than the corresponding figures with Level A of environmental variability, shown in the 5th paragraph above. Thus the greater the “accidental” fluctuations in reproduction, the more benefit is to be derived from close regulation of fishing and escapement—which seems reasonable enough. At the same time, the fishery becomes very variable from year to year, particularly with A-type populations.

Observe also that, with this kind of regulation, *the more variable the “environment”, the greater is the long-term average catch*, for any given reproduction curve and given replacement level of abundance (compare Tables VII and V). This result springs basically from the fact that the effects of environmental changes are considered to be multiplicative, whereas the catches are averaged arithmetically.

CONDITIONS WHEN LOW LEVELS OF STOCK HAVE A VERY POOR RATE OF REPRODUCTION (POPULATION G)

Population G (Fig. 2) has a reproduction curve of a type demonstrated by Dr. F. Neave to be characteristic of stocks of pink and chum salmon, possibly other salmon as well. In this type of curve there is a secondary reduction in reproductive rate at really low levels of spawning stock, and the population, if once reduced to that level, produces only a slender percentage surplus each year.⁵ However, near "normal" stock densities there is a satisfactory excess of reproduction over escapement.

Curve G, as drawn, has the same maximum equilibrium yield point as Curve A—at a spawning density of 0.43, and with a yield equal to 0.33 of the replacement stock. The important difference between G and A is that G has very poor resistance to exploitation at low stock densities. If environmental variability reduces the stock to such a level, it is in a dangerous situation unless fishing intensity is substantially relaxed. Specifically, if the spawners are reduced below 0.34, the stock can no longer completely compensate for exploitation at the rate of 43% and soon becomes extinct if the fishery is maintained at that intensity. This in fact happens when either level A or level B of random variation is applied to Curve G, without changing the rate of exploitation from what is optimum for a stable environment: spawners are reduced to less than 1% of replacement and catch becomes negligible after 9 or 10 generations.

EFFECTS OF REGULATION. As could be anticipated, the situation described by a Type G curve is one where selective regulation is particularly desirable. Using the plan where escapement has first claim on all fish up to 0.43 (the spawning stock needed for maximum sustained yield), but that otherwise the 43% rate of exploitation prevails, the situation is as in Table VIII. The progressive decline to extinction is avoided, and the stock produces an average catch equal to or (at Level A) slightly more than what is obtained when there is no environmental variability (Table II), though there is large variation from year to year. The average catch and range of catches at Level A is exactly as for Population A (Table IV).

When optimum regulation is applied—the fishery taking everything above 0.43—the result is as in Table IX. With the smaller variability Curve G produces very little less than does Curve A (Table V), but with the larger variability it produces 25% less (Table VII). In either case the yield is still substantial, averaging 30% more than the 0.33 obtained yearly when there is no environmental variation.

COMMON EXPLOITATION OF DIFFERENT STOCKS

Consider a fishery which acts on four populations characterized by the reproduction Curves A, B, C and H of Fig. 1 and 2. The four populations are taken to be of equal size under conditions of no fishing: that is, the replacement

⁵ In a more extreme case the curve might fall below the replacement diagonal, and the population at low densities would be critically unstable even without any fishing.

level of stock is the same for all. In spite of their original equal abundance, the four have very different potentialities from the fisherman's point of view. Exploitation at various levels gives the catches shown in Fig. 4. The catches for the equilibrium exploitation of the stocks A-C are calculated from (A17) and (A19) of Appendix I of Ricker (1958), while for stock H corresponding expressions were developed from our expression (2).

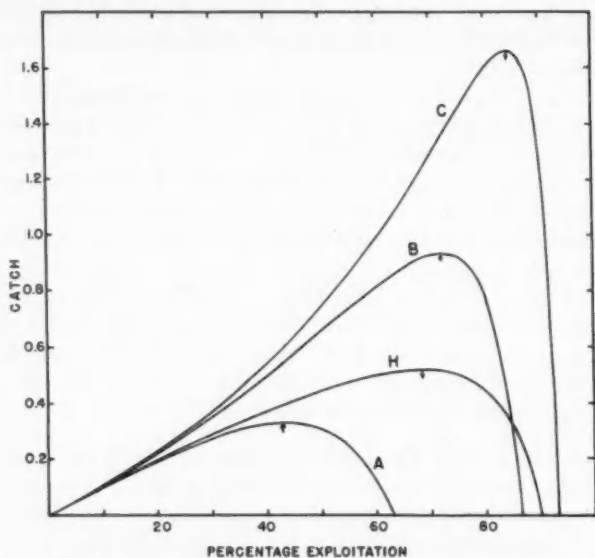


FIG. 4. Sustained yield at various rates of exploitation, for populations A, B, C and H of Fig. 1 and 2.

The maximum sustained yield for Population C is 5 times that for A, B being intermediate. Also, these three populations produce their maximum equilibrium catches at very different rates of exploitation: 43% for A, 72% for B and 84% for C. Population H, described by a curve of a different family from the other three, has its maximum equilibrium catch at 68% removal (Table II).

If the stocks above can be fished separately, the possibility exists of taking the best equilibrium catch from each one, and hence the maximum catch in all. However, it often happens that several stocks are mixed in a common fishery and must be subjected to approximately the same rate of exploitation.

Some combinations of three of the catch series of Fig. 4 are shown in Fig. 5. Considering combinations of two stocks at a time, either of two situations may occur: (1) the maximum yield may be available at an intermediate level of exploitation, so that both components persist (e.g., Curve A + B); or (2) maximum yield may be achieved only at a level of exploitation which exterminates one of the two stocks, the remaining one contributing solely to the fishery (Curve A + C). Also, if all three of A, B and C must be fished in common, it would pay

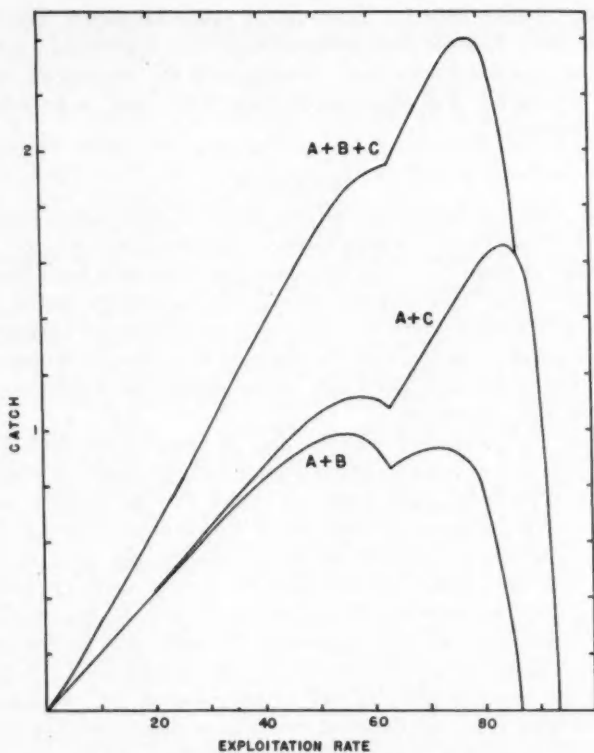


FIG. 5. Sustained yields when three combinations of populations A, B and C are exploited in common.

to fish at a level which exterminates A (Curve $A + B + C$). Observe that the combined graphs are not smooth curves, but have a reentrant near the rate of exploitation at which any stock can no longer persist.

There seems little reason to doubt that different stocks of salmon are characterized by different reproduction potentialities, even though the three models that are combined above may represent a fairly extreme contrast. In general, then, a non-selective fishery, attacking a number of stocks equally, might very well exterminate one or more of the runs which originally existed in a given region, as an unavoidable by-product of developing the fishery up to the point of maximum sustained yield. Conversely, if maximum yield is the objective, any adjustments of gear, fishing season or fishing boundaries are desirable which will promote individual exploitation of the separate units of a mixed commercial stock, when these differ in reproductive potential.

The above conclusions are based on the situation where the stocks adhere strictly to their density-dependent reproduction curves. However, the previous

analysis showed that, over the fairly broad range examined, variability of the environment often does not change the *average* yield appreciably, and even when it does, the change is not very large. Consequently the conclusions of this Section will apply reasonably well when stocks vary from year to year because of a variable environment.

DISCUSSION

1. Most of the conclusions arrived at from the analyses above could, I believe, be reached by "intuition" or common-sense reasoning, without any actual computation. Many of them have long been used by those who have been managing salmon fisheries. The value of these calculations and others similar is mainly to provide objective models which can be cited in justification of a particular regulation. What is simple common sense to one man may seem ridiculous to another. The calculation of benefits and losses under prescribed conditions is the only way to resolve such arguments.

2. It may be questioned whether the 24 generations used above are a sufficiently long random series to give adequate average results. A longer sequence would certainly be better, and plans are under way to program an electronic computer to handle problems of these sorts. However, it is very unlikely that a really long sequence of generations would change any part of the picture appreciably. For one thing, the sequence of factors used in Table I, when multiplied together, is almost equal to 1, so that there is no appreciable excess of favourable or unfavourable effects. Another consideration is that most of the comparisons made above are between two or more stocks all of which have been subjected to *the same* variability; and to some extent the peculiarities of the random series used affect the different stocks in similar ways. Finally, a number of tests were run using only 12 instead of 24 generations, and even these gave very similar comparisons.

3. The models used above apply directly to stocks in which fish are vulnerable to fishing during only one year of their life history, and all at the same age. In British Columbia this is true of pink salmon, and it is well approximated by cohoes and some sockeye stocks. When maturity occurs importantly at two or more ages, the calculation can be modified quite easily to cover this eventuality, provided each fish becomes vulnerable only once (as in all Pacific salmon) or if this is approximately true (many stocks of Atlantic salmon). In such stocks, of course, effects of random variations tend to be "averaged out" and the fishery is less variable, from year to year, than it would otherwise be.

In most fisheries, however, the fish are vulnerable in quantities for more than one year of the life of the individual fish. Here computations like the above are possible, but the regulation of such stocks involves an additional consideration—that of harvesting the stock at the best ages as determined by the balance between natural mortality and growth. This may indeed often be the most important consideration. It is when a mixed-age stock, say of a trout or a flatfish, exhibits several years of declining recruitment, that the question of whether the spawning stock is too small (or too great) is most apt to arise, along with the

question of whether a trend in environmental conditions might not be responsible for the decrease.

4. How realistic are the two levels of environmental variability used above? Wickett (1958) feels that the recruitment obtained from a given number of pink and chum salmon spawners on the central British Columbia coast can vary over a range of at least 24:1; our "Level B" of random factors spans the range 18:1 in 24 years. Reproduction of sockeye, coho and Atlantic salmon, on the other hand, seems more stable, and the "Level A" range of variability, 7:1, would include most of the observations. Individual streams or nursery grounds, of course, tend to be more variable than large statistical areas. On the whole, however, one or other of the two levels of environmental variability used in these models would be close to conditions actually observed in our salmon fisheries.

5. The use of a random selection of normally-distributed fluctuations for these models is not meant to imply that natural fluctuations in reproduction are necessarily of this kind. Insofar as it depends on temperature and rainfall, success of reproduction may exhibit as much or as little in the way of consistent *trends* as does the weather, and hence be predictable to the same degree. As a practical matter at the present time, however, the kinds of weather which affect Pacific salmon reproduction have not been shown to have recognizable trends, certainly none that are predictable in advance; so the random-series model seems the best kind to use for this group of fish.

6. A point of considerable importance to fishermen is the fact that regulation for maximum long-term average catch introduces greater instability into the year-to-year picture. Without giving it too much thought, it might have been supposed that achieving maximum yield would make catches more uniform from year to year. Actually, management for maximum total yield makes catches *more variable* from year to year, and in some cases it is required that fishing be stopped altogether in quite a number of seasons. If a group of fishermen depend on a single stock of a single species, such stoppages could be disastrous for them, and regulation for a smaller grand average catch might well be adopted in such a case. More often, other species or other stocks are available to a fisherman in a given year. Nevertheless everyone is naturally disappointed and inclined to be critical when a normally large run fails to show up, and most or all of what does appear has to be used for escapement.

However, far from indicating defective management, large fluctuations in catch and (sometimes) complete closures of fishing are actually a necessary condition for obtaining maximum average yield from our salmon fisheries.

SUMMARY

1. As compared with uniform conditions for reproduction and survival, a variable environment results in variable recruitment to a stock each year; making the catch fluctuate if rate of exploitation is the same in all years. These fluctuations are greatest when the fish are caught as they approach maturity and do not survive from one spawning to the next, particularly if the catch is substantially of a single age. Such species are examined in this paper, using numerical models.

2. The best *constant* rate of exploitation when stocks fluctuate (over the range examined here) is the same as or very close to the best rate when there is no environmental variation. At this rate the environmental variability may decrease average catch, may increase it, or may leave it unchanged, depending on what type of curve describes the population's average net reproduction potential at various densities of spawners. If there is an increase or decrease in average catch, it is not very great.

3. A fairly substantial increase in average catch can be obtained by decreasing fishing intensity when the stock is small so as to let a larger fraction of the stock become spawners. The average net gain is the greater, the greater is the environmental variability. (Type G reproduction is an exception to this, but the extinction of the stock which selective regulation avoids would have been more rapid at the higher level of variability.)

4. Somewhat greater average catches are obtained if, in addition to the above, the rate of exploitation is increased in years of large stock, so that not more than the mean optimum number of fish is allowed to spawn. The increases in average catch obtained in this way (over conditions of a constant rate of exploitation) vary from 26% to 81% with different reproduction curves, using the greater of the two levels of environmental variability of Table II. With the lesser variability, the increases range from 12% to 49%.

5. With reproduction of type G (Fig. 2), reduction in fishing in years of poor supply is absolutely essential if the stock and fishery are to survive. Continuous use of the rate of exploitation which is best for conditions of stable reproduction will quickly exterminate a type G stock when the environment is as variable as those used here.

6. In general, regulation of a fluctuating stock for maximum long-term average yield unavoidably means increasing the year-to-year variability in yield. The smaller catches are decreased, and in some situations complete closures are necessary in certain years if the long-term maximum is to be obtained.

7. When a number of stocks of differing reproduction potentials are mixed in a common fishery, maximum sustained yield may in some cases be obtained only by fishing at a rate which exterminates one or more of them. A larger total yield is always obtainable when each such different stock can be fished and regulated separately.

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TABLE II. Maximum equilibrium catch, rate of exploitation, and size of spawning stock, under conditions of no environmental variability, for the six populations of Fig. 1 and 2. (In this and later Tables, catch and stock are expressed as fractions or multiples of the replacement level of stock—that which would exist in the absence of fishing and in a stable environment.)

Population	Maximum equilibrium catch	Rate of exploitation at m.e.c.	Size of spawning stock at m.e.c.
		%	
A	0.330	43.3	0.433
B	0.935	72.2	0.361
C	1.656	84.1	0.314
F	0.760	78.3	0.210
H	0.520	68.4	0.240
G	0.330	43.3	0.433

TABLE III. Mean catch and range of catch for five populations when subjected to random variability of Level A (Table I), and when rate of exploitation remains as in Table II.

Population	Mean catch	Range
A	0.33	0.09-0.90
B	0.94	0.31-2.13
C	1.66	0.62-3.67
F	0.71	0.22-1.65
H	0.58	0.20-1.25

TABLE IV. Mean catch and range of catches with Level A of environmental variability, when available stock up to the optimum size of spawning population is reserved for escapement, and the fishery can take the surplus but not to exceed the rate of exploitation of Table II (for the stock as a whole).

Population	Mean catch	Range	Years with no catch
			%
A	0.36 ^a	0-0.88	21
B	1.01	0.21-2.33	0
C	1.79	0.47-4.12	0
F	0.86	0.22-1.89	0
H	0.61	0.10-1.30	0

^aIn this and later tables, the years of no catch are included in finding the average.

TABLE V. Mean catch and range of catches with Level A of environmental variability, when available stock up to the optimum size of spawning population is reserved for escapement, and the fishery takes all the remainder.

Population	Mean catch	Range	Years with no catch
			%
A	0.45	0-1.44	33
B	1.15	0.20-2.87	0
C	1.99	0.55-4.61	0
F	0.92	0.21-2.21	0
H	0.65	0.09-1.66	0

TABLE VI. Mean catch and range of catches with Level B of environmental variability, when rate of exploitation is fixed at the optimum value shown in Table II.

Stock	Mean catch	Range
A	0.33	0.03-1.07
B	0.93	0.14-3.12
C	1.64	0.27-5.72
F	0.73	0.08-2.35
H	0.68	0.10-1.96

TABLE VII. Mean catch and range of catches with Level B of environmental variability, when available stock up to the optimum size of spawning population is reserved for escapement, and the fishery takes all the remainder.

Stock	Mean catch	Range	Years with no catch
			%
A	0.59	0-2.15	42
B	1.51	0-4.80	4
C	2.55	0.24-7.57	0
F	1.20	0.06-3.67	0
H	0.86	0-2.80	8

TABLE VIII. Mean catch and range of catches for Population G (Fig. 2), at two levels of environmental variability, when available stock up to the optimum size of spawning population (0.43) is reserved for escapement, and the fishery can take the surplus but not to exceed a rate of exploitation of 43.3% (for the stock as a whole).

Environmental variability	Average catch	Range	Years with no catch
			%
Level A	0.36	0-0.87	21
Level B	0.33	0-1.30	42

TABLE IX. Mean catch and range of catches for Population G, at two levels of environmental variability, when the available stock up to the optimum size of spawning population (0.43) is reserved for escapement, and the fishery takes all the remainder.

Environmental variability	Average catch	Range	Years with no catch
			%
Level A	0.44	0-1.45	33
Level B	0.44	0-2.15	42

Spawning Stock Size and Resultant Production for Skeena Sockeye¹

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ABSTRACT

For age 4 and 5 Skeena sockeye, plots of total production of adults from individual brood years against number of parent spawners gave a reproduction curve with an almost linear ascending limb and a very precipitous descending limb. Maximum reproduction (2.4 million sockeye) was achieved at spawning levels of slightly over 0.9 million; the maximum sustained yield (1.4 million) was provided by spawnings of 0.9 million. The stock is very sensitive both to small changes in fishing intensity, and to random variations in survival caused by density-independent environmental fluctuations. Therefore the attainment of high sustained yields by application of a constant optimum exploitation rate is not practical. Regulation to provide the optimum number of spawners each year would more likely provide the highest average yield. Observed fluctuations in commercial catches over the past 50-odd years can be accounted for by changes in annual rates of exploitation. Still higher yields might be attained if individual components of the composite stock studied could be managed separately.

INTRODUCTION

THE SKEENA RIVER is currently the third largest producer of sockeye salmon (*Oncorhynchus nerka*) in British Columbia. Over the past 50 years it has produced an average annual yield to the fishery of 79,439 48-lb. cases of sockeye, or about 953,000 individual sockeye per year. The Skeena sockeye are exploited mainly by gill-nets within a radius of 40 miles of the river mouth and within the lower reaches of the river itself. In the Skeena River system there are some 16 lakes which support sockeye. Of these, by far the most important is the Babine-Nilkitkwa watershed which accommodates about 75% of the annual escapement to the Skeena system as a whole.

Past studies (Milne, 1955; Godfrey, 1958) have shown that there is a positive relationship between the size of the catch in the parent year and the contribution of progeny of that year to the commercial catch. This relationship suggests that the number of adults returning to the fishery from a given brood year may be dependent upon the abundance of spawners in the parent year. The purpose of the present paper is to examine the available information in more detail and to characterize the relationship, if any, between the abundance of spawners and the size of the resulting stock.

HISTORY OF THE FISHERY

The history of the Skeena sockeye fishery, from its inception in 1877 up to 1948, has been described in detail by Milne (1955). It began in 1877 with the establishment of the first cannery. In that year about 3,000 48-lb. cases of sockeye (approximately 37,500 fish) were packed, and about 40 boats were

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employed. From 1877 to 1910, the number of boats and canneries increased progressively, the expansion in effort being rewarded with increasing returns (Fig. 1, Table I). In the peak year 1910, a catch of 185,000 cases (about 2,750,000 sockeye) was obtained by a fleet of some 850 gill-netters.

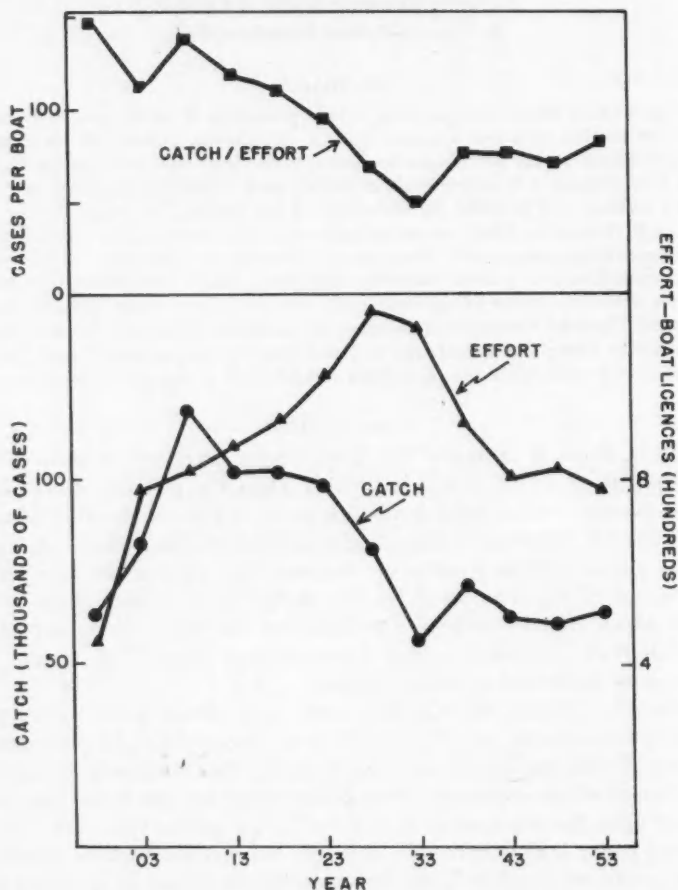


FIGURE 1. Catch, effort, and catch per unit effort for Skeena sockeye, 1896 to 1955 (averaged in 5-year periods).

During the early period of expansion, the increasing exploitation of salmon stocks throughout British Columbia prompted application of conservation measures. By 1894, province-wide regulations had been issued covering the licensing of boats, the type of gear to be used in fishing, and the areas in which fishing was permitted. From 1900 to 1910 concern over the heavy fishing in the Skeena area resulted in a limitation of the number of licences issued to 850 per

season, and to stricter enforcement of existing regulations concerning the area of fishing (see figure 1 of Milne, 1955) and the time of fishing (a 24-hour weekly closed period existed during this period).

Beginning in 1915, the number of boats was permitted to increase again and, by 1933, a peak total of 1,218 boats was licensed to fish the Skeena. Not only did the number of boats increase but, from 1924 to 1935, the mobility of the fleet was greatly increased by the replacement of sails by gasoline engines. To counter the increase in effort increasingly stringent regulations were imposed. During the period 1910 to 1936, the upriver boundary had been moved about 8 miles seaward and the weekly closed period had been lengthened from 24 to 48 hours.

From 1910 to 1936 both the catch and the catch per unit effort declined steadily so that, during the 5-year period from 1931-1935, the annual average pack was about 56,000 cases, only 46% of that obtained during the peak 5-year period, 1906-1910 (Fig. 1).

Due largely to the poor return per boat in the mid-1930's, which made maintenance of a large fleet impractical, the number of boats fishing began to drop after 1935 and, by 1941-1945, the fleet averaged only 803 boats per year, compared to the peak average of 1,175 per year in 1931-1935.

Following this decrease in number of boats fishing, the catch climbed slightly and, for the 1941-1945 period, an average annual catch of some 62,000 cases was obtained. With the decrease in number of boats, there was an increase in catch per unit effort of about 50%.

From 1936 to 1954 both the average catch and the average catch per boat remained relatively constant at about 50% of what prevailed during the peak period 1906-10. The catches from 1955 to 1957 were much lower than any since 1885. These lower catches were due to severe restriction of the fishery during the years of return of progeny from broods depleted by the 1951-52 rock slide in the Babine River (Godfrey *et al.*, 1954, 1956).

From 1941 to the present the gear and boats have continued to increase in effectiveness. In 1942 the mechanical drum, which greatly speeds the picking up of nets and permits the fishermen to make more sets, was adopted by the fleet. In 1955, nylon gill-nets, which are said to be about twice as effective as other nets for river fishing, replaced linen nets. These increases in effectiveness were again accompanied by increased restriction. In 1949, the upstream boundary was moved 3 miles farther seaward. In 1953, a special one-week closure was imposed near the peak of the run. During the period 1955-1957 there have been a number of special closures of the fishery during the fishing season, and an extension of the basic weekly closed time from 48 to 72 hours.

In assessing variations in fishing effort, an important consideration in the long-term development of the Skeena fishery has been the participation of fishermen of Japanese origin. As demonstrated by Milne (1955), Japanese have been more effective fishermen than either whites or Indians. Their greater effectiveness is due to the fact that they fish more days of each fishing season and more hours per day. In the early part of the century Japanese fishermen formed a major component of all British Columbia gill-net fishermen. For example, in 1916, 2,506 of

TABLE I. Estimates of catch, escapement, and total returning stock for Skeena 4₃ and 5₂ sockeye, 1902 to 1957, and estimated units of effort and computed exploitation rates, 1908 to 1957. Where there is no entry, data are not available.

Year	I	II	CATCH		V	VI	EFFORT				X	XI	XII	SPAWNING ESCAPE- MENT			XV	XVI	
			III	IV			Total 4 ₁ +5 ₂	Total boats	Japanese boats	Gas boats				Drum boats	Total boats (weighted)	Instan- taneous			Annual a
			thousands of fish			boat licence units					thousands of fish								
1902		cases																	
3		117,677	0	0	
4		50,968	0	0	
5		93,404	0	0	
6		84,717	781	...	0	0	
7		86,394	870	...	0	0	
8		108,413	700	...	0	0	
9		139,846	1,527 ¹	863	518 ²	0	0	1,010	0.80	0.55	1,124	1,138	520	1,658			
1910		87,901	960 ³	850 ³	510 ³	0	0	994	0.79	0.55	706	575	1,805	2,380			
1		187,246	2,045 ³	850 ³	510 ³	0	0	994	0.79	0.55	1,506	613	1,308	1,921			
2		131,066	1,431 ¹	850	510 ³	0	0	994	0.79	0.55	1,064	781	1,239	1,487			
3		92,498	626	413	1,039	850	510 ³	0	0	994	0.79	0.55	765	513	381	894			
4		52,927	316	286	602	850	510 ³	0	0	994	0.79	0.55	444	1,062	675	1,737			
5		130,166	337	993	1,330	850	510 ³	0	0	994	0.79	0.55	979	1,775	1,882	3,657			
6		116,553	461	772	1,233	962	577 ³	0	0	1,126	0.80	0.59	771	953	1,207	2,160			
7		60,923	282	252	534	868	521 ³	0	0	1,015	0.80	0.55	393	273	177	450			
8		65,760	552	198	750	788	473 ³	0	0	922	0.73	0.52	623	575	273	848			
9		123,322	994	378	1,372	889	533 ³	0	0	1,040	0.82	0.66	970	1,603	849	2,452			
1920		184,945	629	1,242	1,871	1,153	692 ³	0	0	1,349	1.07	0.66	868	1,847	1,991	3,838			
1		90,869	161	712	873	954	572 ³	0	0	1,116	0.88	0.59	546	782	841	1,623			
2		40,018	368	113	481	1,109	665 ³	0	0	1,298	1.03	0.64	244	849	447	1,296			
3		100,615	1,010	172	1,182	1,091	642	0	0	1,271	1.00	0.63	625	1,093	394	1,487			
4		131,731	1,053	484	1,537	900	578	0	0	1,070	0.85	0.57	1,043	1,213	284	1,497			
5		144,732	438	1,115	1,553	941	385	18	0	1,022	0.81	0.56	1,098	389	469	858			
6		77,785	501	496	997	1,067	327	65	0	1,115	0.88	0.59	624	1,141	1,205	2,346			
7		82,307	656	268	924	1,129	295	75	0	1,158	0.91	0.60	554	1,084	498	1,582			
8		83,988	752	244	996	1,195	295	162	0	1,227	0.97	0.62	549	920	424	1,344			
9		34,524	245	179	424	1,208	295	257	0	1,249	0.99	0.63	224	482	197	679			
		77,714	696	286	982	1,143	295	263	0	1,192	0.94	0.61	565	336	341	677			

1930	130,952	694	771	1,465	1,202	295	637	0	1,287	1.02	0.64	742	617	364	981
1	93,029	552	299	851	1,076	295	607	0	1,171	0.92	0.60	510	518	371	889
2	52,624	290	263	562	1,119	295	760	0	1,226	0.97	0.62	310	1,136	420	1,556
3	27,693	215	126	341	1,218	295	669	0	1,304	1.03	0.64	173	420	220	640
4	54,558	389	215	604	1,164	295	740	0	1,264	1.00	0.63	320	626	594	1,220
5	52,879	316	222	538	1,053	295	842	0	1,177	0.93	0.61	310	850	333	1,183
6	81,960	670	219	889	970	295	882	0	1,108	0.88	0.59	2,156	788	2,944	1,202
7	41,023	231	231	462	850	295	840	0	997	0.79	0.55	340	763	439	1,202
8	46,988	382	134	516	1,049	295	1,043	0	1,196	0.94	0.61	297	227	308	535
9	68,388	459	321	780	844	295	841	0	1,922	0.78	0.54	588	273	1,045	1,318
1940	116,505	1,229	190	1,419	926	295	922	0	1,073	0.85	0.57	963	683	1,602	2,285
1	81,183	450	465	915	981	295	976	0	1,128	0.89	0.59	572	486	697	1,183
2	29,976	111	215	326	775	0	774	774	860	0.68	0.49	305	356	549	905
3	28,259	131	148	279	749	0	749	749	831	0.66	0.48	272	171	306	477
4	67,855	321	491	812	725	0	725	725	805	0.64	0.47	824	2,163	993	3,156
5	103,940	243	801	1,044	787	0	787	787	874	0.69	0.50	940	218	577	795
6	52,928	89	450	539	877	0	877	877	973	0.73 ^a	0.52 ^a	486	334	778	1,112
7	32,511	58	319	377	750	0	750	750	833	0.69 ^a	0.50 ^a	307	397	514	911
8	101,268	1,125	159	1,284	833	0	833	833	925	0.73	0.52	1,066	1,846	581	2,427
9	65,937	125	569	694	886	2	886	886	985	0.81 ^a	0.55 ^a	480	759	604	1,363
1950	47,479	105	389	494	800	90	800	800	938	0.73 ^a	0.52 ^a	382	430	171	601
1	61,694	219	429	648	791 ^a	...	791	791	...	0.78 ^a	0.54 ^a	163	61	123	184
2	114,775	949	264	1,213	860 ^a	...	860	860	...	0.73 ^a	0.52 ^a	158	421	216	637
3	65,003	342	262	604	813 ^a	...	813	813	...	0.62 ^a	0.46 ^a	701	524
4	60,817	206	289	495	778 ^a	...	778	778	...	0.70 ^a	0.50 ^a	510
5	14,649	24	93	117	663 ^a	...	663	663	...	0.76 ^a	0.53 ^a	100
6	14,663	126	19	145	0.30 ^a	0.26 ^a	361
7	25,428	191	73	264	0.43 ^a	0.35 ^a	448

¹Estimated assuming 10.9 4₂ and 5₂ fish per case (the average number of 4₂ and 5₂ fish per case for the 1916-1925 period).

²Assuming that 60% of the gill-net licences were issued to fisherman of Japanese origin (see text, p. 1012).

³No record available. Boat licences were assumed to be 850.

⁴See Table II.

⁵Licences no longer issued by area. Boat figures derived from Fishery Officer's estimates of number of boats fishing.

⁶Derived from catch, escapement statistics similar to those in Table II.

the 4,615 gill-net licences issued in the province were taken out by Japanese fishermen (Anon., 1918, p. 240). On the Skeena, although accurate records are not available for the years prior to 1922, it is probable that about 60% of the gill-net fleet was manned by Japanese. Between 1922 and 1926 the number of Japanese fishermen was reduced by licence limitations from about 60% of the total Skeena fishermen to about 35%; and from 1926 to 1941, when the total licences issued for the Skeena varied between 844 and 1,218, the number of licences issued annually to Japanese remained at 295. In 1941, as a consequence of wartime regulations, all Japanese left the Skeena area. They began to return to the Skeena fishery in 1949 and at present again form a substantial segment of the Skeena gill-net fishermen.

ESTIMATION OF STOCK SIZE AND ABUNDANCE OF SPAWNERS

In order to determine the relationship between the number of spawners and the resultant total stock, it is necessary to obtain two pieces of information: first, the abundance of the total stock returning from the seeding of a given year; and second, the number of fish spawning in the parent year. To estimate the magnitude of the total returning stock, it is necessary to determine the contribution of each brood year to both the commercial catch and the escapement. On the Skeena, sockeye predominantly mature at 4 and 5 years of age. Thus the total stock of returning adults produced by the spawners in year n would be the number of 4-year-old fish in both the catch and escapement in the year $n + 4$ and the number of 5-year-old fish in the catch and escapement in year $n + 5$. Data on both the magnitude of the commercial catch and on its age composition are available since 1912. However, reliable data on the abundance and age composition of spawners are available only since 1946 (e.g. Brett, 1952).

ESTIMATES PRIOR TO 1946 AND IN 1948

Without direct measures of the characteristics of the spawning populations prior to 1946, it becomes necessary to estimate the size of annual sockeye escapements and their age compositions by indirect means. For the years in question, such estimates could be derived if the annual rate of exploitation and the number of fish in the catch, and the age composition of both the catch and escapement, were known.

ESTIMATION OF ANNUAL EXPLOITATION RATES

For the period 1946 to the present, relatively accurate estimates of the rate of utilization and the age composition of the escapement are available from catch statistics and from examination of fish on the spawning grounds. The number of boats fishing on the Skeena is also known for this period. If it is assumed that the instantaneous rate of fishing in any year is proportional to the number of boats operating in that year, and knowing the number of boats operating in both the recent and earlier periods, it is possible to estimate annual exploitation rates in years prior to 1946.

In establishing the rate of exploitation in recent times, it is necessary to restrict consideration to years in which the pattern of the fishery (with respect to length of fishing season and to duration of weekly closed periods) was essentially similar to that which existed in the pre-1946 period, and in which reliable measures of the size of spawning escapements were available. The years 1946, 1947, 1949, and 1950 fulfil these requirements.² Estimates of the rate of exploitation and instantaneous rate of fishing for these years are given in Table II (columns VII and VIII). From these data it is seen that in the years in question the rate of exploitation averaged slightly over 50%.

In determining the number of units of effort (here the number of boats fishing) for each year, the number of licences issued (see Table I) can be used as the measure of the number of boats fishing each season. However, because the effectiveness of gear has varied over the period under study, and because the proportion of Japanese fishermen also has changed, direct use of boat licence data would provide biased measurements of rates of exploitation. It is therefore necessary to adjust the boat licence data for changes in fishing effectiveness of gear and fishermen. Milne (1955) has examined the comparative effectiveness of fishermen of different racial origins and of the effectiveness of gasoline boats (commonly called 'gas' boats) as compared to sail boats, and has used these data to arrive at weighted measures of fishing effort (adjusted numbers of boats). He accepts as his unit of effort 1 gas boat operated by a white or Indian fisherman. To account for the lesser effectiveness of sail operations he applies a factor of 0.9 to sail boats and to adjust for the greater effectiveness of the Japanese, applies a factor of 1.5 to all boats operated by Japanese licence holders. Because the introduction of mechanical net drums occurred suddenly (in 1942), there are no data available to assess the difference in effectiveness between boats equipped with drums and others. However, the increased effectiveness of drum operation is provided primarily by the ability of the operators to haul their nets more quickly and thus to make more sets per unit time. This advantage is very similar to that conferred by the addition of the gas engine to the old sail boat hulls, in permitting gas boat operators to make more drifts over favoured fishing grounds (bars) per unit time. Without more precise data it is most reasonable to assume that mechanical-drum gas boats had about the same degree of increased effectiveness over non-drum gas boats. Thus, a factor of 1.11 would be assigned to drum-equipped boats.

In Table I, the number of gill-net boats licensed for the Skeena area since 1908 are listed (column VI). By applying the factors described in the foregoing paragraph, weighted numbers of boats have been derived and are given in column X of Table I.

Using these weighted numbers of boats as the measure of effort, estimates of the rates of exploitation for the period 1908-1945 and in 1948 were derived as

²Escapement estimates are not reliable for 1948 (due to a washout of the Babine adult counting weir), nor in 1951 and 1952 (due to the destruction of a large part of the escapement by the Babine River rock slide). From 1953 on, the seasonal pattern of the fishery has been altered by a series of special closures and strikes.

TABLE II. Rates of utilization and fishing effort for Skeena sockeye; 1946, 1947, 1949 and 1950.

I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Year	Commercial catch	Indian ¹ catch	Spawning escapement	Total ² escapement (III+IV)	Total stock (II+V)	Rates of utilization ⁴ (II/VI)		Boats	Japanese boats	Weighted boats ³	Unit rate of fishing (VIII/XI)
			thousands of fish			a	i	no.	no.	no.	c
1946	644	39	555	594	1238	0.52	0.73	877	0	973	0.00075
1947	385	41	345	386	771	0.50	0.69	750	0	833	0.00083
1949	766	48	569	617	1383	0.55	0.81	886	2	985	0.00082
1950	527	43	443	486	1013	0.52	0.73	800	90	938	0.00078
Average						0.52	0.74	828		938	0.00079

¹Catch of sockeye in Indian food fisheries above the commercial fishing boundary.²Total escapement is composed of all fish escaping the commercial fishery (i.e. catch of upstream Indian food fishery plus spawners).³During this period all boats were equipped with mechanical drums. Appropriate weighting factors have been applied (see page 1013).⁴The annual rate, *a*, is the catch divided by the total stock; the instantaneous rate, *i*, is equal to $-\log_e(1-a)$.

follows: In the period 1946-1950, for which the rate of exploitation is known with some precision, the average rate, 52.3%, was effected by an average of 932 weighted boats.³ Converted to an instantaneous rate of fishing, this exploitation rate becomes 0.740. Thus the average instantaneous rate of fishing per boat is calculated as $0.740/932 = 0.00079$. In column XI of Table I the weighted boat values have been multiplied by this estimated unit rate of fishing to arrive at estimates of the total rate of fishing in each year. In column XII these are converted to arithmetic rates of exploitation (fraction of the population caught).

These rates of exploitation were computed without regard to the possible influence of changes in fishery regulations on the effectiveness of the fleet. The main changes during the period under study were movements of the up-river fishing boundary (in 1925, 1935 and 1948). Available data indicate that the changes that did occur probably did not exert extreme effects on effectiveness. For example, the rate of exploitation prior to the 1948 boundary change was very similar to that observed in the period immediately following the shift (Table II). As a consequence, no corrections have been made to the effort data to account for changes in regulations in the pre-1946 period.

ESTIMATION OF AGE COMPOSITION AND CATCH ABUNDANCE

In studying the relation between the abundance of the total stock and the size of parent spawning escapements, it would be expected that the most precise relationship would be achieved if statistics for a single stock could be employed. As mentioned earlier, however, the Skeena sockeye population is composed of several different stocks and precise separation of the single most important stock (that of the Babine-Nilkitkwa area) is not possible. Nevertheless, differences in the age composition of the runs to some lakes permit some restriction in the number of stocks that must be treated as a unit.

Examination of the age composition of the catches (summarized annually in the British Columbia Provincial Fisheries Reports, 1912 to 1957) indicate that the majority of adult sockeye in the catch are 4- and 5-year-old fish that have spent one year in fresh water (4_2 's and 5_2 's). However, every year there are also substantial numbers of fish of 5 and 6 years of age that have spent two years in fresh water (5_3 's and 6_3 's). Recent observations of scales from fish taken on the spawning grounds indicate that most of these 5_3 's and 6_3 's spawn in the Morice and Alastair Lake systems and that the runs to these two areas contain relatively few 4_2 and 5_2 individuals. The spawning runs to Morice and Alastair Lakes have comprised, on the average, about 13% of the total Skeena spawning escapement in recent years. Of sockeye utilizing the remaining lake systems, about 85% utilize the Babine-Nilkitkwa watershed. Thus, if the 5_3 and 6_3 fish are omitted from estimations, the resultant relationship between escapement and return will reflect more accurately the performance of the single most important stock in the Skeena system.

³Correction factors used in Table I were also applied in column XI of Table II.

In Table I, columns III and IV, the estimated numbers of 4₂ and 5₂ fish in each year's catch are listed and the total given in column V. These data were derived using essentially the same method as was outlined by Godfrey (1958, p. 333). However, some adjustments were made to correct for errors in sampling procedures. In the early years especially, it was found that sampling was not carried out in proportion to seasonal changes in the abundance of the catch. To correct for this, the annual age compositions were recalculated by weighting the observed weekly estimates of age composition according to the weekly abundance of the catch. In general, these recalculations necessitated only relatively small changes in earlier estimates of age composition (e.g. Godfrey, *loc. cit.*).

ESTIMATION OF SPAWNERS AND RETURNING STOCK

With the above information on the rates of exploitation, data on the abundance and age composition of the catch may now be utilized to provide estimates of the abundance of spawners in the years prior to 1946 (and 1948), and of the abundance of the returning stock produced by the spawnings of those years.

Estimates of total escapements in the pre-1946 period and in 1948 would be derived as follows:

$$(1) \quad E_n = C_n \left(\frac{1-a}{a} \right)$$

Where: E_n = total escapement in year n ,

C_n = total catch in year n (4₂'s and 5₂'s),

a = annual rate of exploitation in year n .

However, the escapement figures derived in expression (1) include a number of sockeye that would be taken in the Indian food fishery before reaching the spawning grounds. In Table III, available data on Indian food catches are compared with the total estimated escapement for the period 1935-1948. The data indicate that during this period the Indian catch comprised 9.2% of the total escapement. To arrive at an estimate of the total *spawning* escapement, it is therefore necessary to apply a factor of 0.9 to expression (1). The size of the spawning stock is therefore calculated as:

$$(2) \quad P_n = 0.9 E_n = 0.9 C_n \left(\frac{1-a}{a} \right)$$

Where: P_n = total spawners in year n .

Estimates of spawning escapements for the pre-1946 period and in 1948 are listed in column XIII of Table I.

For the pre-1946 period and for 1948, the total resultant stock (i.e. the catch and the escapement arising from the spawning in a given brood year) was estimated as follows:

$$(3) \quad S_n = \frac{C_{4n+4}}{a_{n+4}} + \frac{C_{5n+5}}{a_{n+5}}$$

Where: S_n = total resultant stock arising from the spawning of year n ,

C_{4n+4} = catch of 4₂ fish in year $n + 4$,

C_{5n+5} = catch of 5₂ fish in year $n + 5$,

a_{n+4} = annual rate of exploitation in year $n + 4$,

a_{n+5} = annual rate of exploitation in year $n + 5$.

Values for S_n are listed in column XVI of Table I.

TABLE III. Total Skeena Indian food catches of sockeye and total estimated escapements of 4₂ and 5₂ fish for the years 1935-48. Catches shown are from data of Pritchard (1948); they exclude catches made on the Bulkley River system, where the sockeye are predominantly 5₂ and 6₂ fish bound for Morice Lake.

Year	Indian catch	Estimated total escapements
<i>thousands of fish</i>		
1935	51	344
1936	99	618
1937	56	378
1938	58	330
1939	71	664
1940	137	1070
1941	58	636
1942	40	339
1943	29	302
1944	48	916
1945	36	1044
1946	28	1185
1947	36	514
1948	30	343
Average	56	620

ESTIMATES FOR 1946 TO 1957 (EXCLUDING 1948)

For the period from 1946 on (except 1948) spawning stock estimates were based on Babine River weir counts and stream survey estimates for all other Skeena spawning grounds except those of Morice and Alastair Lakes.⁴ Total escapements from the commercial fishery were derived by adding the spawning ground estimates to Indian food catches (excluding those taken on the Bulkley River, migration route for Morice Lake spawners). The estimates of spawning escapements are listed in column XIII of Table I.

Examination of length frequency distributions of spawning fish to obtain gross indices of age composition indicates, that in most years, the age composition of the spawning stock roughly paralleled that of the commercial catch. However, in the years 1946, 1947 and 1950, there was apparently a higher proportion of 4₂'s in the escapement than in the catch. For the period 1946-1954 the age composition of the escapement was taken to be the same as that in the catch, except for the 3 years mentioned above, for which the proportion of 4₂'s in the escapement was

⁴See p. 1015.

adjusted upward. From 1955 to 1957, special closures of the fishery (as mentioned earlier) distorted the normal seasonal pattern of fishing, making it impossible to use catch age composition data for estimating age composition of spawners. In these years, age composition data concerning the escapement were derived by examination of scales from samples of sockeye taken by a research boat fishing throughout the season above the commercial fishing boundary.

From these data the contributions to both the catch and escapement, of the spawning in a given brood year, were determined and the estimates listed in columns XIV, XV and XVI of Table I.

RELATION BETWEEN SPAWNERS AND RESULTING STOCK

For the period 1908-1957, estimates have been derived of the annual abundance of spawners and of the total stock of returning adults produced from these spawnings. Consideration has been restricted to 4₂ and 5₂ fish, which are predominantly sockeye originating in a single large lake system, the Babine-Nilkitkwa. In Fig. 2, the estimated number of fish produced from the spawnings of individual brood years is plotted against the abundance of spawners in the parent year. A diagonal line has been drawn to indicate the locus of points wherein the total resultant stock would just equal the number of fish spawning in the parent year. Hence, points lying above this "45-degree line" represent cases where the total resultant stock was greater than the number of parent spawners, and points below the line indicate brood years in which the total return was less than the number of spawners in the parent year.

In general, the return and the number of spawners have tended to vary together; small spawnings have tended to provide small returns, and, although the resultant stocks vary widely at high spawning levels, the largest returns have been obtained from larger—though not the largest—seedings. In only two brood years of the 45 examined were the returns smaller than the number of parent spawners. In other words, in only two years did the spawning stock fail to replace itself.

To characterize the relationship described above, the points have been fitted empirically by the trend line shown in Fig. 2. This line was derived by ranking escapement-return data according to the abundance of spawners (net escapement), then by determining the moving mean by fives for associated escapement-return values. The moving mean values of the resultant stock were then plotted against the appropriate moving mean values for the parent escapements, and a line drawn by eye through the points (Fig. 3).

The shape of the trend line in Figures 2 and 3 indicates that, for spawning escapements from 0.2 million to 0.9 million increasing escapements on the average provided increasing returns. Between 0.9 and 1.0 million spawners, the maximum return was achieved; at escapement levels beyond 1.0 million, the absolute magnitude of the return decreases.

The above relationship indicates that, for that portion of the Skeena stock under study, the abundance of spawners is one of the most important factors determining the production of sockeye. The almost direct linear relation between spawning population and average return in the ascending limb of the curve

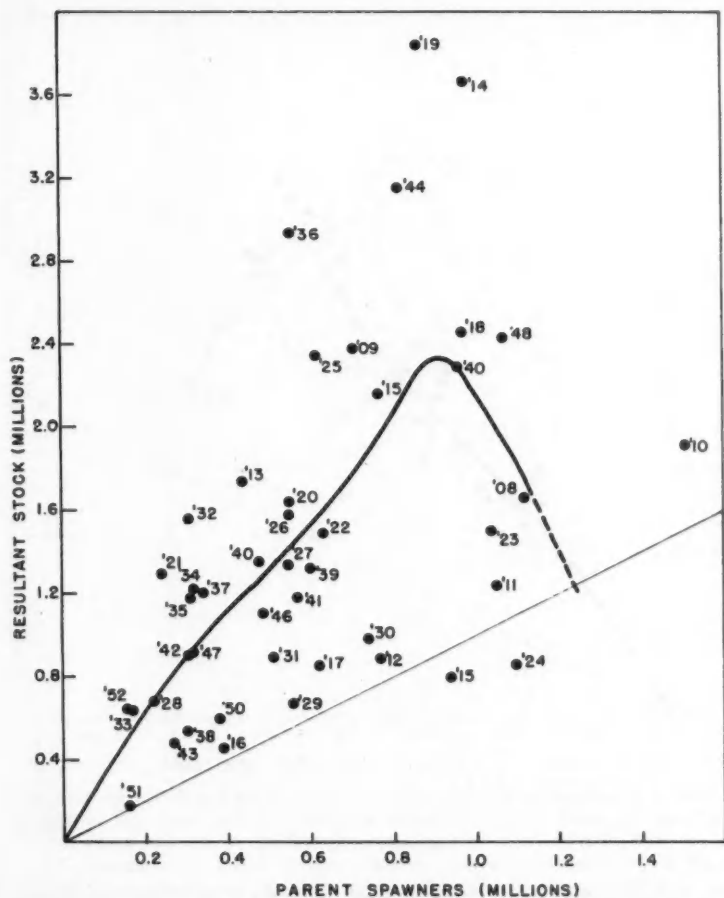


FIGURE 2. Numbers of 4_2 and 5_2 Skeena sockeye (catch plus escapement) plotted against numbers of parent spawners. Figures in the body of the graph indicate brood years. For the trend line, see Fig. 3.

indicates that for spawning populations up to 0.9 million, the capacity of the environment to produce sockeye is not limiting. However, the decrease in the size of the average return in the upper part of the curve strongly suggests that the capacity of the environment to produce sockeye is exceeded at spawning levels beyond 1.0 million.

It is probable that limitation of production at high population levels occurs during the early freshwater history of the sockeye. This limitation could either take place on the spawning grounds or in the lake nursery area. Although there are no data available to indicate that the Skeena spawning beds have been over-taxed, the amount of spawning area available to the fish is finite, and it is

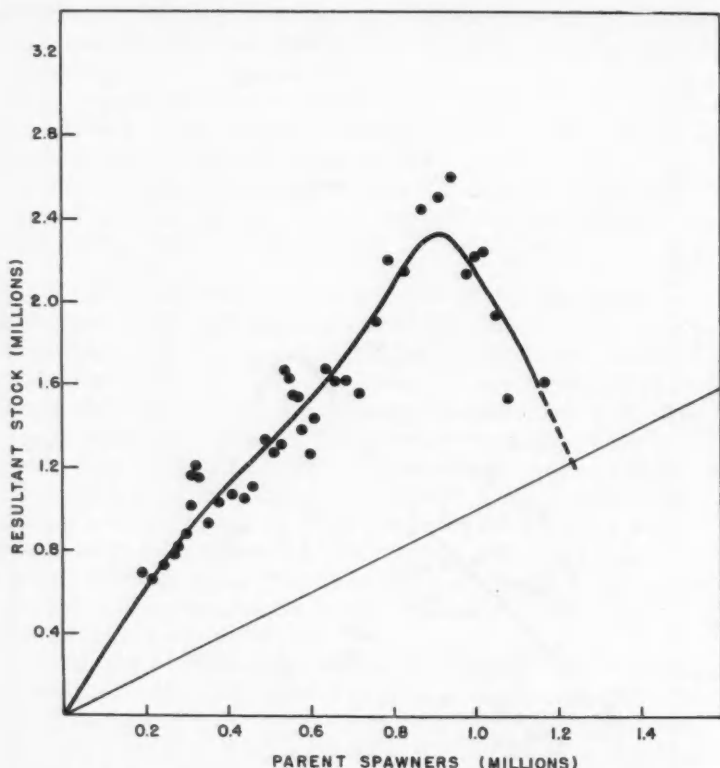


FIGURE 3. Coordinates of moving means (by fives) of ranked parent spawner and total resultant stock data, to illustrate derivation of the trend line in Fig. 2 (see text, p. 1018).

possible that in some years over-seeding may have occurred. Evidence has recently been provided to indicate that the lake nursery area of some parts of the Babine-Nilkitkwa system is sometimes sufficiently densely populated by young sockeye to result in a decrease in growth rate (Johnson, 1956). As indicated by Foerster's (1944, 1954) work at Cultus Lake, such reduction in growth (presumably as a consequence of competition for food) may result in a lowering of survival rate and a proportionately poor return of adults.

In examining the spawner-return relationship in Fig. 2, it is evident that the individual points scatter widely about the trend line. At spawning levels in the region of the ascending limb of the curve, the deviations of the observed returns from the trend line are smallest near the origin and tend to increase with increasing spawners. In Fig. 4 the data used in Fig. 2 have been plotted on a double logarithmic scale. Here it is seen that the logarithms of the deviations from the trend line are no greater at high spawning levels than at lower levels, indicating that the proportional variation is the same throughout the range of spawnings up

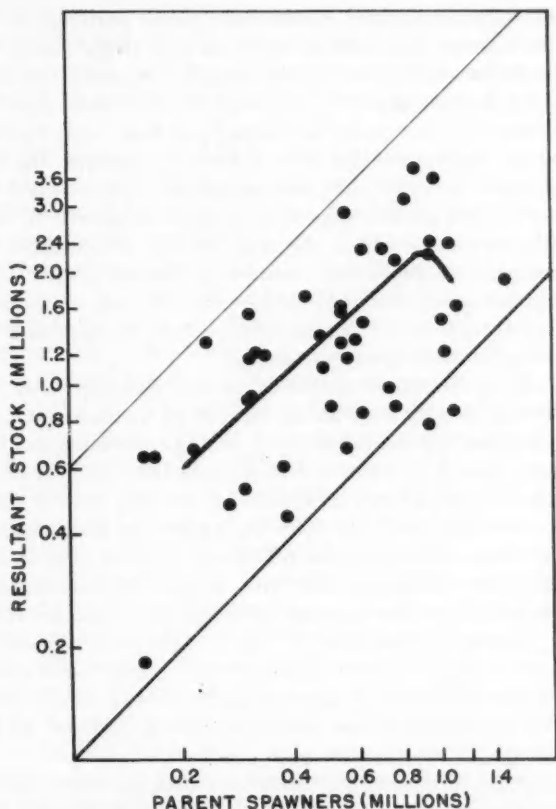


FIGURE 4. Double logarithmic plot of resultant stock against parent spawners for 4_2 and 5_2 Skeena sockeye. The lower diagonal line is the replacement line; the upper diagonal line represents the approximate upper limit of variation of the points. The trend line between diagonals was transposed directly from the trend line in Figures 2 and 3.

to 0.9 million. This pattern of variation probably results from the influence of randomly fluctuating environmental conditions which affect the survival of the sockeye independently of their abundance. Such factors would affect both large and small populations in the same proportionate manner. Examples of such factors might include adverse temperatures, or scouring of spawning grounds by floods, both of which would probably destroy the same proportion of deposited eggs whether the spawning were sparse or dense.

SPAWNER ABUNDANCE, EXPLOITATION AND YIELD

The curve derived in Fig. 2 reflects the performance of 4_2 and 5_2 Skeena sockeye over the past half century. As outlined earlier, these fish originate

primarily in the Babine-Nilkitkwa system and for the purposes of the foregoing development have been considered as members of a single stock. However, the sockeye of the Babine-Nilkitkwa system actually comprise several individual runs, each having its own spawning area and characteristic time of migration. For some of these runs, the young live throughout their early freshwater life in separate basins of the system (Johnson, 1956). In general, the early-running fish tend to populate the large main area of Babine Lake, whereas later-running fish are primarily destined for spawning grounds adjacent to the outlets of Babine and Nilkitkwa Lakes. Thus, the curve in Fig. 2 represents the spawner-return relationship for a population containing several stocks, each of which would have its own spawner-return relationship. In any one year, the stocks may each be responding to a different relative level of spawning density with respect to the capacity of its own environment.

Prior to 1954, the seasonal pattern of fishing was such that all important segments of this mixed stock were fished with about the same intensity. Recently however, it has become apparent that the spawning escapements of early running stocks to the main basin tributaries of Babine Lake have been much smaller than those which would result in full utilization of the lake nursery area (Johnson, 1956). For this reason, in 1956 and 1957 the fishery has been closed during the early part of the season, disrupting the traditional seasonal pattern of fishing that had existed during the previous 50-odd years. If such regulations are effective in increasing production from this segment of the Babine-Nilkitkwa stock, then the spawner-return relationship indicated in Fig. 2 might be significantly altered.

Even though, as suggested above, changes in the traditional seasonal pattern of fishing might alter the shape of the composite curve, it nevertheless describes the responses of the mixed stock under the rather uniform seasonal fishing conditions⁵ existing until very recent times.

Ricker (1954) has discussed the use of reproduction curves for studying the relationship between spawner abundance, exploitation and yield. In Figures 2 and 3, the height of the derived spawner-return curve above the replacement line indicates the number of fish in the returning stock that would be available for fishing if the number left to spawn in the years of return were to just equal the number of parent spawners. For example, in Fig. 2, when the parent spawners number 1.0 million, total returning stock would average about 2.2 million. If in the year of return an escapement equal to that of the parent year were to be allowed, then the fishery could take $2.2 - 1.0 = 1.2$ million fish. In Fig. 5a, estimated average yields for various numbers of parent spawners are illustrated. Since the total harvest is shared between the commercial fishery and the Indian food fishery, two yield curves have been shown; the top line representing the total yield and the bottom line indicating that part of the yield taken by the commercial fishery⁶ alone. The data show that the maximum average total yield would be obtained from spawnings in the order of 0.9 million. Of the total yield of 1.4

⁵Cannery records and records of regulations as far back as 1917 indicate that the seasonal patterns of catch and effort did not change greatly from 1917 until recent times.

⁶The yield to the commercial fishery is estimated by assuming that the Indian fishery take is equal to 10% of the total escapement from the fishery.

million fish, the commercial fishery would take about 1.3 million. Spawning escapements greater and less than 0.9 million provide smaller average yields. As suggested by Fig. 5b, at spawning levels above about 1.25 million fish, the spawning stock would fail to reproduce itself and thus there would be no surplus for fishing⁷.

Ignoring the effects of random environmental variations, the stock would be stabilized at various spawning levels by the imposition of different steady rates of exploitation (Ricker, 1954). In Fig. 5, the equilibrium points for various rates of exploitation are indicated by arrows.

Because the ascending limb of the reproduction curve is nearly straight, minor variations in the rate of exploitation would theoretically bring about drastic changes in the level at which the stock would stabilize. Thus, if the estimated commercial fishing exploitation rates varied in the relatively narrow range between 57% and 67%, the stock could reach equilibrium at spawning levels anywhere between 0.1 and 0.9 million spawners, with yields between 0.2 million and 1.3 million. This means that at commercial exploitation rates in the vicinity of 60%, the stock is very sensitive to small changes in fishing pressure. Since the maximum sustainable yield would be obtained theoretically by a commercial rate of exploitation in this same general range (57% as indicated in Fig. 5b), the problems involved in attempting to crop the stock at the optimum level through providing a constant annual rate of exploitation would be very great.

If the steady rate of exploitation were to exceed 70% for any considerable period, the stock would be reduced to a level close to extinction.

At commercial exploitation rates below about 57%, the stock would stabilize at levels of spawning associated with the descending limb of the curve. In this area, the curve is not particularly sensitive to minor changes in fishing pressure, but because of its precipitous slope would be very sensitive to random variations which provided higher returns than the average; i.e. if, with constant fishing rates below about 50%, fortuitous environmental conditions made the returning stock greater than expected, the resultant run would be pushed further down the descending limb and the return in the next generation would be drastically reduced.

As illustrated by Ricker (1958), when year-to-year variations in the success of survival are considered, the average yield obtainable from fish stocks is usually greater if the fishery is regulated to provide the optimum number of spawners rather than to apply the best constant rate of exploitation. This is especially true of sensitive stocks like the Skeena sockeye, where modest deviations from the average magnitude of the returning run can cause disastrous declines in yield if a constant fraction of the stock is taken every year. Furthermore, even if the returning stock conformed exactly to Fig. 3, it would in practice be very difficult to maintain the rate of exploitation within the narrow range required to provide a high yield. Thus best management of the Skeena stock involves varying the rate

⁷For the sake of simplicity in this discussion, the fish are considered to return to spawn at a single age. Values obtained for *average* yield under different fishing intensities and at different parent spawning levels are the same whether the returning stock is considered to be composed of one or several age-classes.

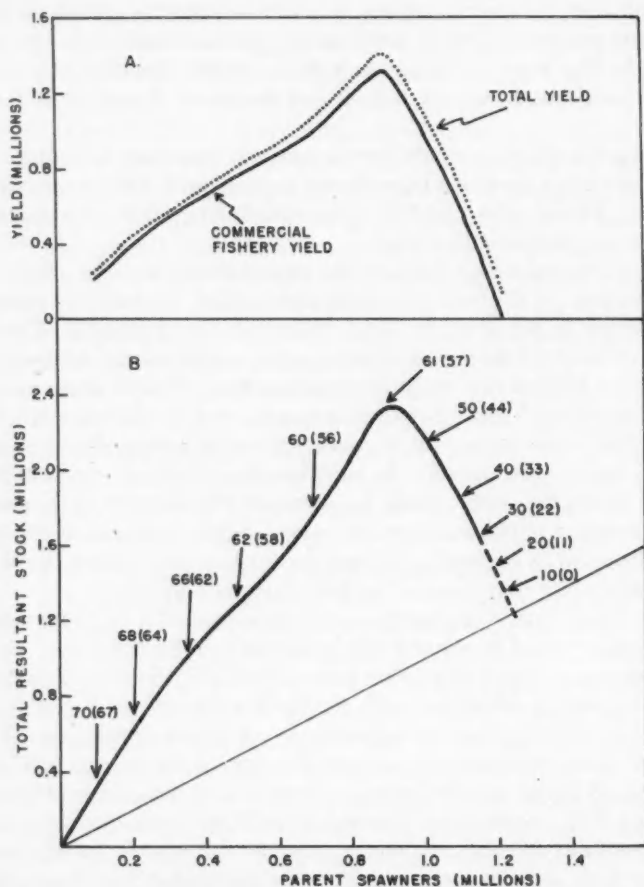


FIGURE 5. Relation between exploitation, stock level, and yield for Skeena 4_2 and 5_2 sockeye. A. Variation in equilibrium yield with size of parental spawning. B. Rate of exploitation, as percentage, associated with stabilization of stock at various numbers of parent spawners. Unbracketed figures in the body of the graph indicate total rates of exploitation (commercial fishery plus Indian food fishery); figures in brackets indicate rates of exploitation exerted by the commercial fishery alone.

of utilization as the size of the stock varies, in order to provide something close to the optimum number of spawners—about 900,000—each year.

Actually, as mentioned earlier, even higher sustained yields might be obtained from the Skeena sockeye population if individual parts of the composite stock (considered as a unit stock in the present paper) were managed as separate units.

The observed fluctuations in the commercial yield of Skeena sockeye over the past 50 years have followed a pattern that would be expected as a consequence of the interaction of the observed changes in rate of exploitation with the

spawner-return relationship. The average yield to the fishery in the period from 1910 to the early-1920's (Fig. 1) remained fairly constant at a level of about 100,000 cases (about 1.0 million fish). The rates of exploitation applied to the parent stocks of these runs hovered around 55%. According to the reproduction curve, commercial exploitation rates of this order would be expected to stabilize the stock at levels near the top of the ascending limb (Fig. 5) and would be expected to provide average yields of about 1 million fish.

From the early 1920's to the mid-1930's the catch fell. In the period during which the parents of the fish contributing to these catches were being exploited, the rate of exploitation had risen to slightly over 60% (Table I), a removal rate which would be expected to move the equilibrium point on the curve toward the left and downward, and to provide smaller yields than in the former period.

From the mid-1930's to early 1940's, the rate of exploitation declined and levelled off in the vicinity of 50%, and the decline of the catch was arrested. The observed respite in fishing increased the average size of the spawning escapements, with the result that the stock would respond by moving upward along the ascending limb of the curve of Fig. 5. However several generations would be required before the stock would become stabilized at higher levels and provide the corresponding average yields.

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The Mark VI Groundwater Standpipe for Measuring Seepage through Salmon Spawning Gravel¹

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ABSTRACT

The groundwater standpipe is a length of pipe, pointed at one end, and has a number of perforations near the point. This is driven into the gravel, where the groundwater flows through it. The permeability of the gravel is measured by lowering the level of water inside the standpipe, one inch below the level outside, and measuring the rate of inflow. The apparent velocity through the gravel is measured in terms of the rate of dilution of a colour solution in the standpipe. A colour is introduced, and its rate of dilution determined from successive small samples taken at suitable intervals of time.

Velocity data from the earlier models were erratic and the permeability calibration did not include the range encountered in nature. In the Mark VI model, the standpipe is open during measurements of permeability. During measurement of groundwater velocity, the colour dilution chamber is completely sealed, colour is introduced and withdrawn through a sphincter valve with a hypodermic syringe. The solution is stirred during the period of dilution.

The criteria of the measurements have been reconsidered. The standpipe, auxiliary equipment, and procedure have been redesigned, and the new model recalibrated. All this resulted in some loss of simplicity, but the data are consistent and accurate within 5%. The equipment is still simple and rugged enough for field examination of salmon spawning redds.

Complete details of design, construction, and procedure, for use in salmon spawning gravels are given in Appendices.

INTRODUCTION

THE FATE OF SALMON EGGS, deposited by the salmon at a depth of about 10 inches into the gravel of a stream bed, depends largely upon the supply of oxygenated water available to them (Wickett, 1954). To estimate the probability of survival

¹ Received for publication May 28, 1958.

of the eggs of a particular redd, or nest, two quantities must be determined—the concentration of dissolved oxygen in the groundwater, and the apparent velocity of the water through the gravel in the immediate vicinity of the redd.

Wickett originated a method of measuring oxygen concentration and apparent velocity, with rugged portable equipment. This was the Mark I standpipe. It was a length of pointed pipe, perforated around its lower end. It was driven into the gravel until the perforated portion was at the average depth of salmon eggs in a redd (10 inches) and the top of the pipe extended above the stream surface. After flushing, a sample of the groundwater was taken for determination of dissolved oxygen. Then a dye (methylene blue) was introduced, and its rate of dilution determined from successive small samples taken at suitable intervals of time.

Pollard (1955) examined the performance of this equipment under controlled conditions. He built a rectangular trough with wire screens near each end. Between the screens he filled it with *random* gravel taken from salmon spawning beds. Flow through the gravel was created by an inflow at one end, and an outflow at the other. The difference of head along the trough was controlled by the relative levels of water in the head and tail-pools which, in turn, were controlled by overflow pipes. The grade line of the water surface in the trough was observed on piezometers tapped into the bottom and sides.

With this equipment he evaluated the relation between the apparent velocity of the water through the trough, and the rate of dilution of the dye in the standpipe. The results with the elementary Mark I model were erratic. To correct this he made a small chamber at the lower end in the region of the perforations. This was connected to the surface by a *small diameter open* pipe. This Mark II standpipe gave somewhat more consistent results.

Pollard examined the theory of seepage through gravel and showed that the velocity is dependent on the hydraulic head and the permeability of the gravel. To determine the permeability he pumped water out of the standpipe and observed the rate at which it flowed in. However, permeabilities were encountered in nature which were beyond the limits of his calibration.

It became necessary, to re-examine the problem and the equipment. This led to considerable modification, and complete recalibration.

The Mark VI Groundwater Standpipe consists of a length of pipe, tipped with steel and perforated around its lower end. The perforated portion can be *completely sealed off* from the upper portion with a liner (called the "velocity liner" because it is used while making velocity measurements). A colour solution is introduced through a sphincter valve, and is stirred, to avoid stratification, while being diluted by the groundwater flow. Samples are withdrawn at intervals with a hypodermic syringe assembly, and compared to standards, to determine the rate of dilution, and hence apparent velocity.

During measurements of permeability, the velocity liner is removed leaving the whole standpipe open. This removes the limit on the rate of pumping, imposed by the small diameter inner tube in the earlier models.

These modifications involved some loss of simplicity which are felt to be warranted by the improvement in results. The final model, the Mark VI Ground-

water Standpipe, incorporates all the principles of the earlier models, but has added features to eliminate the sources of error. It gives consistent results which are reliable within 5%. This is satisfactory in view of the variability of conditions in nature, which may be as great as 100% at nearby points in a single redd.

The body of this paper discusses the critical considerations of measurement of seepage velocity and permeability which led to the modifications of the standpipe. The details of design and procedure are given in the Appendices.

THEORY OF FLOW THROUGH GRAVEL

The apparent velocity of a liquid through a porous medium is the rate of seepage, expressed as volume of liquid per unit time, crossing a unit cross-section, of solids plus voids, normal to the direction of flow.

$$V = \frac{Q}{A} \quad (1)$$

where V is apparent velocity, Q the volume of flow per unit time, and A is the total cross-sectional area. In this paper the term "velocity" shall mean apparent velocity. The true velocity is the actual velocity through the interstitial spaces. The units used will be centimeters per hour (cm./hr.)

The hydraulic gradient (S) is the slope of the water surface.

$$S = \frac{\Delta h}{L} \quad (2)$$

where Δh is the difference in height ($h_1 - h_0$) in a distance L , in the direction of flow. It has no units.

Pollard (1955) showed that, for the laminar flow occurring at the velocities usually encountered in spawning gravel, D'Arcy's coefficient of permeability, or more simple the permeability, K , as defined by

$$K = \frac{V}{S} \quad (3)$$

is independent of the apparent velocity, V . Permeability depends only upon the composition and degree of packing of the gravel, and upon the viscosity of the water, which in turn depends upon the water temperature. He also showed that the permeability is inversely proportional to the kinematic viscosity of the water.

It will be noted that since the gradient, S , is dimensionless, the permeability, K , will have the same units as velocity, i.e. cm./hr.

DIRECT MEASUREMENT OF PERMEABILITY

A slightly modified version of the horizontal flow, open trough permeameter described by Pollard was used (Fig. 1). It was a rectangular trough with a gravel retaining screen near each end. Piezometers tapped into the walls indicated the water levels from which the gradient was computed. To improve the readability, all piezometers were connected by T's and rubber tubing to a common line. They were normally isolated by pinchcocks. The common line led to a glass reading tube, set at a slope of one unit vertical distance in 10 units slope distance. This

PERMEAMETER

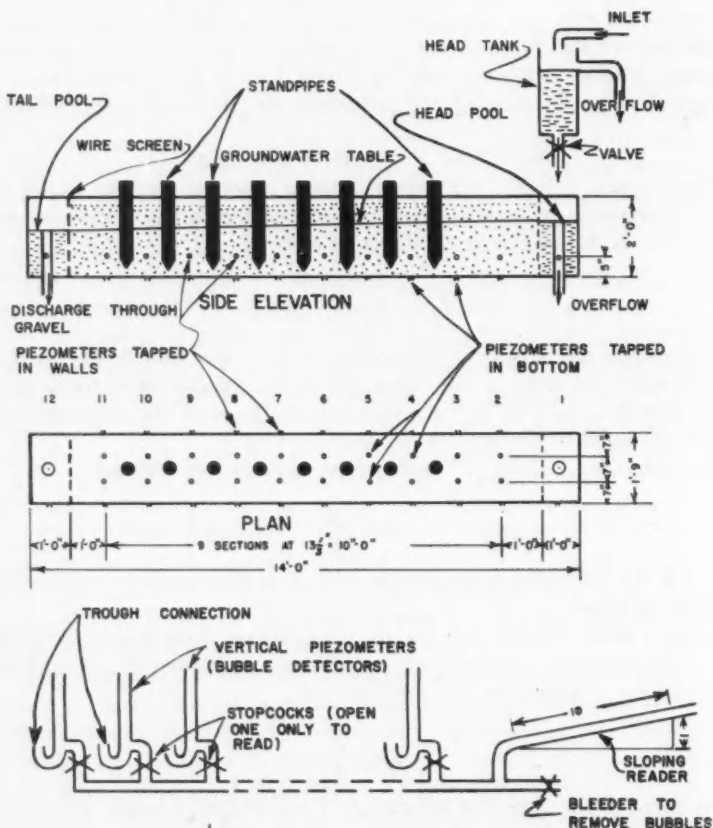


FIG. 1. Schematic diagrams of the permeameter and piezometer connections.

reading tube was backed by a meter stick. By releasing the pinchcock on any piezometer, the corresponding level could be easily read to 0.1 mm., i.e. 1 mm. on the meter stick. To equalize temperature-density effects, the reading system was allowed to come to room temperature before each set of readings was taken. Provision of a constant level head tank in the supply line to the permeameter made it possible to keep fluctuations of discharge rate to less than 1 per cent.

The permeameter was filled between the screens with carefully graded and mixed gravels, to achieve permeabilities as uniform as possible throughout the trough. The volume rate of flow, Q , was measured by collecting discharge water

through timed intervals. The wetted cross-section area, A , was taken as the width of the trough multiplied by the average height of the water level, determined on the piezometers. The difference in hydraulic head, Δh , was the difference of readings between piezometers numbers 2 and 11.² The distance, L , between these piezometers was measured. From these values the permeability, K , was determined by combining equations (1), (2) and (3).

$$K = \frac{V}{S} = \frac{Q/A}{\Delta h/L} \quad (4)$$

A mean value of K from a statistically significant number of successive determinations was adopted as the criterion for each gravel examined. These data are shown in Table I.

TABLE I. Permeabilities of gravels reduced to 10°C. (T5 was the first gravel used after adoption of final standpipe design and procedure.)

Gravel	Number of determinations	Mean \bar{K}_{10} and Probable Error
		<i>cm./hr.</i>
T5	11	5,100 ± 50
T6	17	615 ± 4
T7	12	79,600 ± 800
T8	14	167 ± 2

INDIRECT MEASUREMENT OF PERMEABILITY

In order to determine velocity with standpipe technique it is necessary to determine permeability. Recent study of the field data has shown that in order to estimate the value of a river reach as a spawning bed it is necessary to make a comprehensive set of measurements, either of the apparent velocities in the gravel, or, if the river gradient is adequate, the permeabilities of the gravel. The permeability of the gravel, the ease with which water can pass through it, may be used as a figure of merit for the gravel—the higher the permeability the greater the supply of oxygenated water that can reach the salmon eggs for a given river gradient.

Pollard (1955) showed that determination of the permeability of spawning gravels by mechanical analyses was impractical partly because of the difficulty of evaluating the degree of packing in the stream bed. Indirect measurement was necessary. He designed a standpipe (Mark II) which partially fulfilled the purpose. It has been redesigned and recalibrated in this research.

This redesigned permeability standpipe, a length of 1½ inch diameter pipe tipped with steel and perforated for its lower 2 inches, is driven into the gravel to a depth of 10 inches as shown in Figure 2. The water level in the pipe is lowered a fixed amount, Δh , and the resulting inflow rate is measured.

² Permeabilities were calculated from readings of piezometers numbers 2 and 11 which were in the gravel, rather than piezometers numbers 1 and 12 which were connected to the tail and head pools. This avoided end effects in the gravel.

PERMEABILITY MEASUREMENT

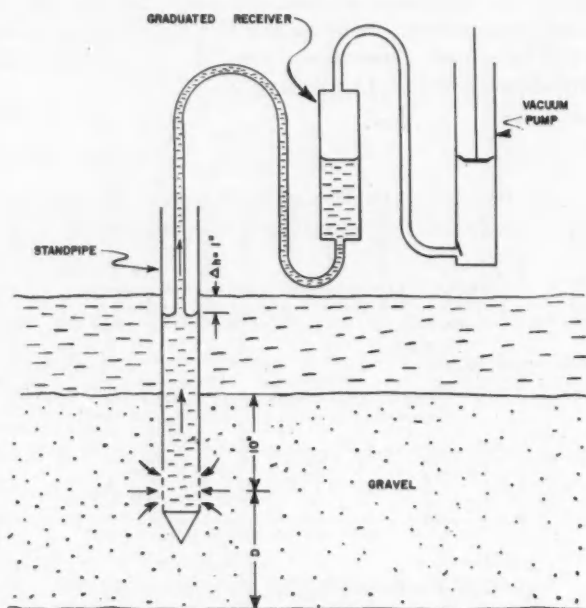


FIG. 2. Schematic diagram of the apparatus and method used for measurement of permeability.

Assuming that the depth, D , (Fig. 2) to the impermeable stratum, below the gravel, is large compared with the dimensions of the perforated chamber, a simple analysis of the analogous problem of a spherical sink will show the dependence of the inflow rate upon permeability, for laminar inflow in a gravel of uniform permeability, K . Referring to Fig. 3, let the apparent velocity of inward flow at a distance r from the center of the sink be V , the radius of the sink be r_0 , and the velocity at the periphery of the sink be V_0 . Let the hydraulic head in the sink be lowered by Δh , and let the head drop across a spherical shell, of radius r , and thickness dr , be dh . Then from continuity:

$$V = V_0 \frac{r_0^2}{r^2} \quad (5)$$

and from the definition of permeability:

$$\frac{dh}{dr} = S = \frac{V}{K} \quad (6)$$

so that:

$$dh = \frac{V_0 r_0^2}{K r^3} dr \quad (7)$$

Integrating, the total head drop is:

$$\Delta h = \frac{V_0 r_0^2}{K} \int_{r_0}^{\infty} \frac{dr}{r^3} = \frac{V_0 r_0^2}{K} \left[-\frac{1}{r} \right]_{r_0}^{\infty} = \frac{V_0 r_0}{K} \quad (8)$$

whence the rate of inflow is:

$$V_0 = \frac{\Delta h}{r_0} K.$$

Thus, for a fixed value of Δh and for fixed dimensions of the perforated chamber, the rate of flow into the chamber is dependent only upon the permeability.

ANALYSIS OF SPHERICAL SINK

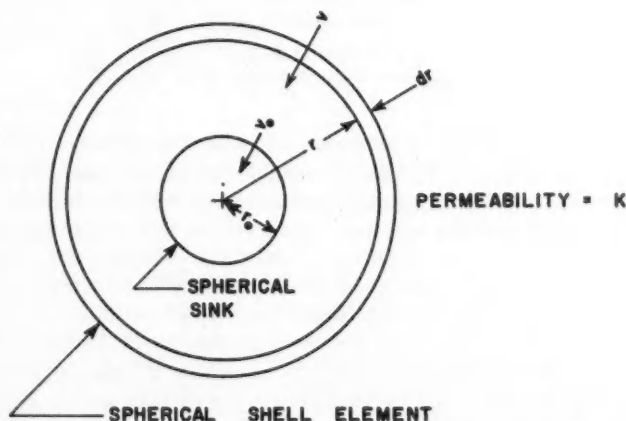


FIG. 3. Diagram for the analysis of the spherical sink problem.

In practice, however, the relationship will not be linear. At high rates of inflow the flow will be partly turbulent, and the size and number of perforations in the standpipe imposes an upper limit on inflow, which a curve of permeability versus inflow will approach asymptotically. Such a calibration curve will also have a positive intercept on the inflow axis because of the slippage of water down the outside of the standpipe.

A calibration curve of permeability and inflow on logarithmic scales, for an instrument of this general design should, therefore, have the shape shown in Fig. 4. Logarithmic scales are used for convenience in plotting the large ranges of values.

SHAPE OF TYPICAL PERMEABILITY CALIBRATION CURVE

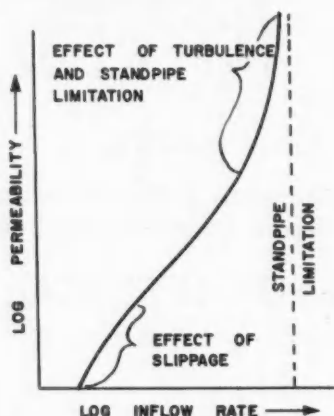


FIG. 4. Anticipated shape of a typical permeability calibration curve.

The discussion of the dependence of inflow upon permeability assumed uniform permeability, which will not usually be encountered. Obviously, some kind of average of the surrounding permeabilities will be obtained. A further analysis of the sink problem will shed light on the nature of this average, and the size of the region that will appreciably affect the measurement. Equation (7) shows that the head drop, for a given thickness of shell, is inversely proportional to the square of the radius of the shell. Thus, the permeability as measured by the standpipe, will be a mean of the average permeabilities of the surrounding shell elements, heavily biased in favour of closeness to the standpipe.

Integrating equation (7) for head drop in a shell between the limits r_0 and r , the head drop, Δh_r , to any radius, r , is

$$\Delta h_r = \int_0^{\Delta h_r} dh = \frac{V_0 r_0^2}{K} \int_{r_0}^r \frac{dr}{r^2} = \frac{V_0 r_0^2}{K} \left[\frac{1}{r_0} - \frac{1}{r} \right] = \frac{V_0 r_0}{K} \left[1 - \frac{r_0}{r} \right] \quad (9)$$

but from equation (8) the total head loss is:

$$\Delta h = \frac{V_0 r_0}{K}$$

Therefore:

$$\frac{\Delta h_r}{\Delta h} = 1 - \frac{r_0}{r} \quad (10)$$

Since the radius of the standpipe is approximately 2 cm., it will be seen that 75% of the head loss occurs within 8 cm. of the center of the chamber, i.e. inside a 6 inch diameter sphere, and from (7) a stone or void at the edge of such a 6 inch sphere will affect a measurement only about $\frac{1}{16}$ as much as a similar stone or void at the edge of the chamber.

In practice, Δh is made to be 1 inch. If too large a Δh is used, the inflow velocities will be high enough to wash the finer particles from the gravel and thereby change the permeability. If this happens, an increase of inflow rates with repeated measurements will occur. Pollard adopted the 1-inch head as a standard, because it was large enough for fairly easy duplication and did not cause a change of permeability.

The change from Pollard's design to a standpipe with a liner, which could be removed for permeability measurements, made it possible to measure higher permeabilities. In the former design, it was not always possible to withdraw water fast enough to maintain the head without creating a partial vacuum in the narrow neck. This caused large fluctuations in the 1-inch head.

EFFECT OF TEMPERATURE

It was pointed out above that the permeability varies inversely as the kinematic viscosity of the water. That is:

$$K'_T = \frac{\eta_T}{\eta_T'} K_T \quad (11)$$

where K_T and η_T are the permeability and the viscosity at temperature T . The prime mark designates a different temperature. This relation may be used to reduce field measurements of permeability to some standard temperature, such as 10°C , for comparison of gravels.

VISCOSITY FACTOR VS OBSERVED TEMPERATURE FOR
REDUCTION OF PERMEABILITY TO 10°C

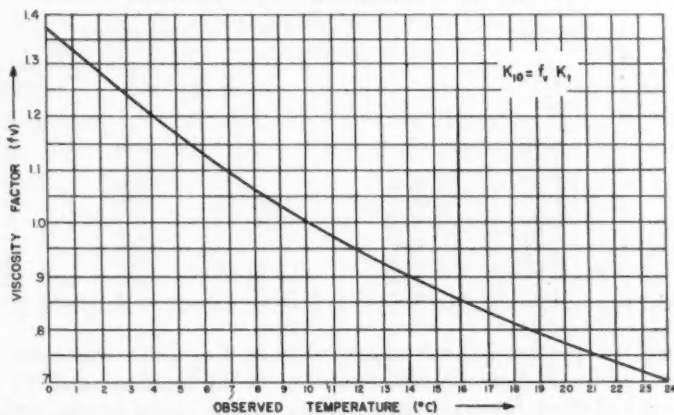


FIG. 5. Viscosity factor versus observed temperature for reduction of permeability to 10°C .

Figure 5 is a graph of viscosity factor:

$$f_v = \frac{\eta_T}{\eta_{10}} \quad (12)$$

plotted against observed temperature, T . From equation (11) it will be seen that multiplying an observed permeability by this factor will reduce it to the permeability at 10°C .

This reduction is applicable only to the permeability as read from the calibration curve, and should only be used to compare gravels. Correction of the inflow rate to the standpipe is not warranted because the relationship of inflow and permeability is not linear. Nor should a permeability, reduced to 10°C , be used to enter the velocity calibration graph. It is the permeability existing at the time of measurement that affects the velocity measurement.

UNIFORMITY OF GRAVELS USED

Pollard's use of *random* gravels, from natural salmon spawning redds was realistic, but did not allow detection of inconsistencies in the performance of the standpipe. Uniform gravels were used throughout these studies, to ensure comparability between the data from the several standpipes, being tested simultaneously in various parts of the permeameter. Each of the gravels was prepared with great care to obtain as uniform permeability as possible, throughout the trough.

Four gravels were used in the calibration. Builders sand was carefully screened into four parts. Their particle size range is shown in Table II. Gravel T5

TABLE II. Mechanical analyses of gravels.

Sieve	Mesh Opening	Percentage retained of the gravels below:			
		T5	T6	T7 (pea gravel)	T8
	mm.				
3-inch	76.2				
1½-inch	38.1				
¾-inch	19.1				
3/8-inch	9.52			9.0	
#4	4.76			86.0	
#8	2.38	43.0		3.6	15.8
#16	1.19	56.3	12.3	0.6	24.2
#30	0.59	0.35	68.4	0.3	17.6
#50	0.297	0.15	17.5	0.2	21.9
#100	0.149	0.10	1.7	0.1	18.3
#200	0.074	0.05	0.05	0.1	2.0
Bottom pan	0.0	0.05	0.05	0.2	0.2

was the coarsest portion, T6 was somewhat finer. Gravel T8 was a mixture of equal parts of T5, T6, and the finest fraction of the builders sand. T7 was a clean pea gravel. Each batch of gravel was thoroughly mixed by the methods of quartering and rolling on a sheet.

PERMEABILITY CALIBRATION

The relation between inflow to the Mark VI standpipe, and permeability in the trough permeameter, was determined by repeated comparisons with several standpipes driven into the gravel in the trough. Since temperatures varied during the observations, each permeability was reduced to the mean temperature, T_1 of the standpipe chambers during the inflow measurements.

The volume of water, v ml., which is withdrawn from the standpipe during an inflow measurement, includes 25 ml., the amount needed to lower the level by 1 inch. The measured collection time, t seconds includes the time, Δt , for pumping this 25 ml. Therefore the true collection rate, Q , used in calibration was:

$$Q = \frac{v-25}{t-\Delta t} \text{ ml./sec.} \quad (13)$$

(for the laboratory equipment Δt was $\frac{1}{4}$ second).

The observed (Q) and the mean (\bar{Q}) rates of inflow to each standpipe in each gravel are shown in Table III. The overall mean ($\bar{\bar{Q}}$) to all standpipes in each gravel was used to prepare the calibration curve.

The variability between standpipes is indicated by the ratio of the mean flow to each standpipe (\bar{Q}) to the overall mean ($\bar{\bar{Q}}$). The probable error in the overall mean ($\bar{\bar{Q}}$) was calculated from all observed inflows (Q). It includes the variability of the gravel and the standpipes.

This measurement is limited by the rate of flow into the standpipe through the perforations near the point. The standpipe was supported in a tank of water and this limit determined.

The data are shown in Table IV, and the calibration curve is shown in Figure 6.

DIRECT MEASUREMENT OF VELOCITY

If the discharge rate of the permeameter is Q ml./hr., the width of the permeameter is W cm., and the average depth of water in the gravel as indicated by the piezometers is H cm., then the mean apparent velocity, V , in the gravel is given by

$$V = \frac{Q}{HW} \text{ cm./hr.} \quad (14)$$

Repeated measurements of the discharge through the permeameter (Q) varied by less than 1 per cent.

INDIRECT MEASUREMENT OF VELOCITY

Velocity measurements with the standpipe are based on the premise that if there is a flow through the surrounding gravel there will be a corresponding flow

TABLE III. Rates of inflow to standpipes, Q , in millilitres per second, with the mean for each standpipe, \bar{Q} , and the overall mean, $\bar{\bar{Q}}$, for each gravel.

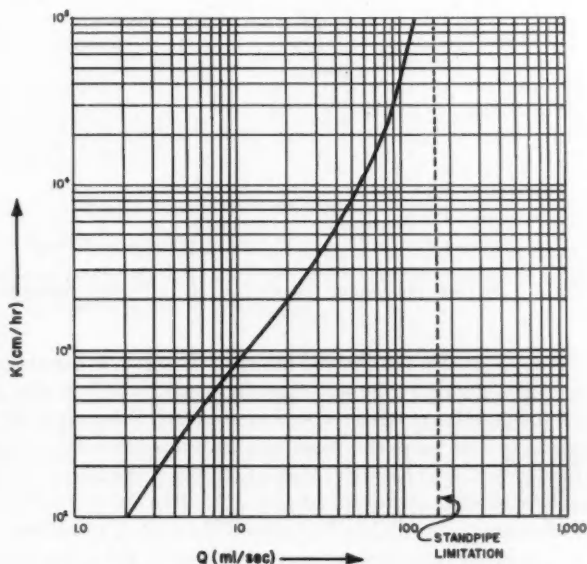
Gravel T5									
Standpipe No.	1	2	3	4	5	6	7	8	All
	47.3	41.1	45.1	42.9	44.9
	49.1	41.5	44.9	41.4	44.8
	46.8	41.0	46.0	40.3	44.4
	48.1	41.3	45.1	40.1	44.3
	49.8	41.3	45.3	39.9	43.9
	49.2	42.0	45.0	42.8	47.3
Mean, \bar{Q}	48.4 ± 0.8	41.4 ± 0.2	45.2 ± 0.3	41.2 ± 1.4	44.9 ± 0.8	44.2 ± 0.4
$\bar{Q}/\bar{\bar{Q}}$	1.09	0.94	1.02	0.93	1.02
Gravel T6									
Standpipe	1	2	3	4	5	6	7	8	All
	8.85	8.35	8.70	9.55	9.05	8.92	8.00	9.48	...
	9.07	8.22	8.50	9.35	8.73	9.22	8.25	9.57	...
	9.03	8.10	8.52	9.43	8.93	9.27	8.38	9.58	...
	9.20	8.00	8.35	9.40	8.90	9.52	8.67	9.62	...
	8.92	7.92	8.28	9.23	9.07	9.72	9.00	9.75	...
	9.00	8.12	8.33	9.43	9.20	9.07	9.00	9.58	...
Mean, \bar{Q}	9.01 ± 0.08	8.12 ± 0.10	8.45 ± 0.13	9.40 ± 0.06	8.98 ± 0.11	9.29 ± 0.19	8.55 ± 0.25	9.60 ± 0.06	8.92 ± 0.05
$\bar{Q}/\bar{\bar{Q}}$	1.01	0.91	0.95	1.05	1.01	1.04	0.96	1.08	...
Gravel T7									
Standpipe No.	1	2	3	4	5	6	7	8	All
	121.0	121.3	121.0	121.7	128.9	127.4	127.9	124.5	...
	122.7	121.7	122.2	122.8	124.8	129.9	128.7	123.9	...
Mean, \bar{Q}	121.8	121.5	121.6	122.2	126.9	128.6	128.3	124.2	124.4 ± 0.9
$\bar{Q}/\bar{\bar{Q}}$	0.98	0.98	0.98	0.98	1.02	1.03	1.03	1.00	...
Gravel T8									
Standpipe No.	1	2	3	4	5	6	7	8	All
	± 2.82	3.14	3.49	3.37	3.50	3.79	3.27	3.44	...
	2.86	3.06	3.67	3.55	3.69	3.59	3.21	3.34	...
	3.02	3.13	3.83	3.43	3.93	3.58	3.36	3.26	...
	3.06	3.22	3.55	3.62	3.49	3.66	3.37	3.28	...
	3.02	3.22	3.68	3.30	3.58	3.62	3.48	3.52	...
Mean, \bar{Q}	2.96 ± 0.07	3.15 ± 0.04	3.64 ± 0.09	3.45 ± 0.09	3.64 ± 0.18	3.65 ± 0.05	3.34 ± 0.07	3.37 ± 0.07	3.40 ± 0.03
$\bar{Q}/\bar{\bar{Q}}$	0.87	0.93	1.07	1.01	1.07	1.07	0.98	0.99	...

TABLE IV. Permeability calibration data. T_1 is the mean temperature of the water in all standpipes during measurements of inflow (Q).

Gravel	Number of standpipes in permeameter	Number of measurements of K by permeameter	Number of measurements of Q per standpipe	Permeability (K_T)	Inflow (Q)	Temp. (T_1)
				<i>cm./hr.</i>	<i>cm.³/sec.</i>	<i>°C.</i>
T5	5	11	6	$6,070 \pm 50$	44.2 ± 0.4	15.7
T6	8	17	6	730 ± 5	8.92 ± 0.05	16.7
T7	8	12	2	$95,600 \pm 950$	124.4 ± 0.6	16.1
T8	8	14	5	201 ± 3	3.40 ± 0.03	16.9
Water	1				160	

PERMEABILITY CALIBRATION

PERMEABILITY (K) VERSUS RATE OF INFLOW (Q)
TO MK VI STANDPIPE AT ONE INCH HEAD

FIG. 6. Permeability (K) versus rate of inflow (Q) to Mark VI Groundwater Standpipe at one inch head.

through the perforated portion of the standpipe (Fig. 7). This can be measured by the dilution rate of a colour solution.

To accomplish this, it is necessary to isolate the region of the perforations as a small chamber, mix the colour uniformly with the water in the chamber and, while maintaining this uniformity, measure the change in concentration over a suitable interval of time.

APPARENT VELOCITY MEASUREMENT

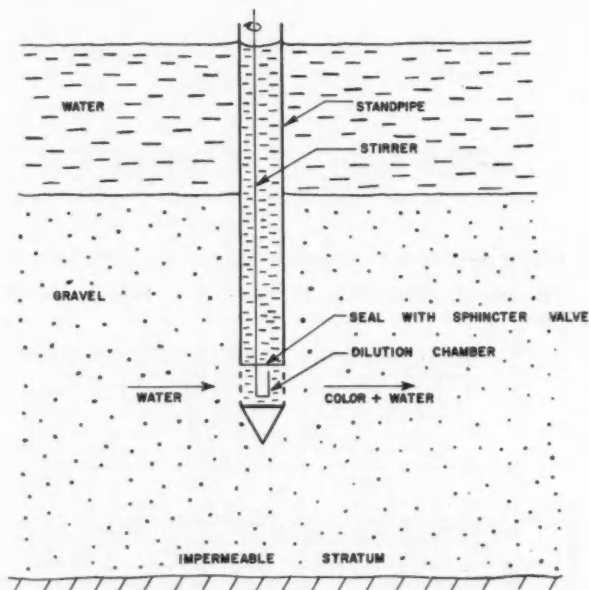


FIG. 7. Diagram illustrating the method of measuring apparent velocity.

In the Mark VI model the 50 ml. dilution chamber is separated from the upper portion of the standpipe by an expanding seal on a "velocity liner" which is lowered into the standpipe with the seal contracted. When it is in position the seal is expanded. In this way, the liner can be lowered without forcing water from the perforations in the chamber. This would wash the fine particles from the gravel in the close vicinity of the standpipe, and alter the permeability.

Two ml. of colour solution are introduced through a sphincter valve in the seal, with a long-shafted hypodermic syringe. A stirrer, incorporated in the liner, prevents stratification of the solution, and keeps it uniform. Samples of the colour solution, withdrawn through the sphincter valve at timed intervals, with a similar syringe, are compared with a set of standards to determine the dilution rate.

DILUTION THEORY

If stirring keeps the solution in the dilution chamber uniform, and the mean velocity across the central vertical cross-section area, A , of the chamber is V_s , then the volume rate of flow through the standpipe is AV_s , and the rate of removal of colour from the chamber is:

$$\frac{dv}{dt} = -\frac{v}{v_s} AV_s = -CAV_s \quad (15)$$

where v is the volume of dye present, C the dye concentration at time t , measured from the start of dilution, and v_s the volume of the chamber.

The rate of change of concentration is then:

$$\frac{dC}{dt} = \frac{1}{v_s} \frac{dv}{dt} = -\frac{1}{v_s} CAV_s \quad (16)$$

If C_0 is the initial concentration:

$$\int_{C_0}^C \frac{dC}{C} = -\frac{AV_s}{v_s} \int_0^t dt$$

whence

$$\ln\left(\frac{C}{C_0}\right) = -\frac{AV_s t}{v_s}$$

and

$$C = C_0 e^{-AV_s t/v_s} = C_0 \left(\frac{1}{2}\right)^{(1.44A/v_s) V_s t} \quad (17)$$

which includes a transformation from the base "e" to the base " $\frac{1}{2}$ ". This facilitates the preparation of standards. Now let:

$$n = \left(\frac{1.44A}{v_s} V_s t\right) + 1 \quad (18)$$

where n is the opacity number, and concentration is measured in terms of n , by comparison with standards prepared for:

$$n = 1, 1\frac{1}{2}, 2, 2\frac{1}{2}, \dots, 8,$$

Since water tends to take the easiest path, it will converge into, or diverge around, the standpipe depending upon whether the permeability of the surrounding gravel is lower or higher than the permeability of the standpipe (Fig. 8). In general, therefore, the velocity in the standpipe, V_s , will not be the same as the velocity in the gravel, V . For a particular gravel permeability, however, we can write:

$$V = a V_s \quad (19)$$

where a is a constant dependent upon the ratio of gravel permeability to standpipe permeability.

FLOW AND HYDRAULIC HEAD LINES NEAR STANDPIPE

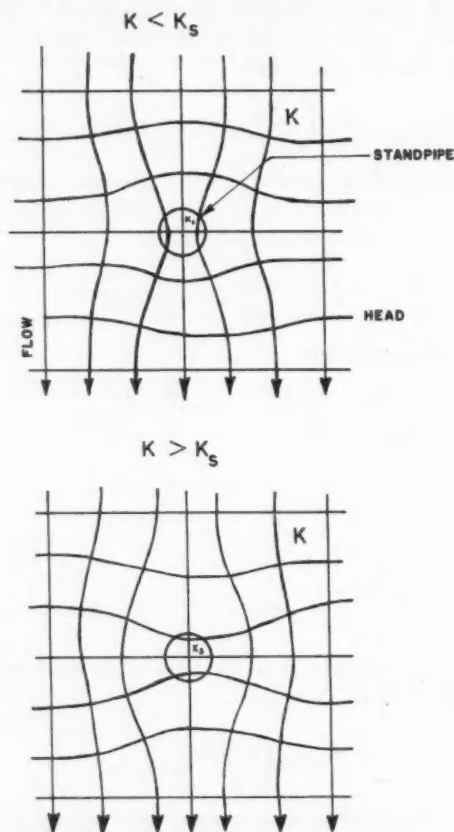


FIG. 8. Diagram illustrating types of flow and contours of hydraulic head near a standpipe.

Combining equations (18) and (19):

$$n = \left(\frac{1.44 a A}{v_s} \right) Vt + 1 \quad (20)$$

Differentiating with respect to time, the dilution rate is

$$\frac{dn}{dt} = \left(\frac{1.44 a A}{v_s} \right) V \quad (21)$$

which is directly proportional to V . That is, the expected result of calibration for velocity against dilution rate is a set of straight lines through the origin, each for

a different permeability, with slopes dependent on the proportionality factor, a . In general, this was confirmed experimentally as shown in Figure 9, which shows apparent velocities in the permeameter plotted against all measured dilution rates for gravel T5³.

VELOCITY AND DILUTION RATE MEASUREMENTS FOR GRAVEL T5

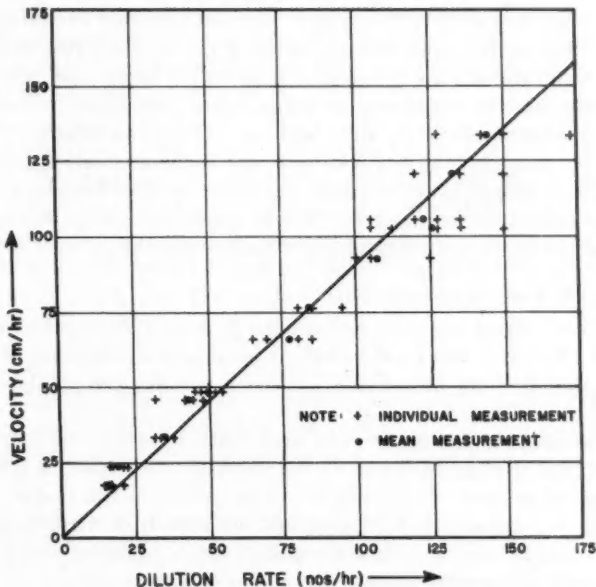


FIG. 9. Apparent velocity and dilution rate measurements in gravel T5.

It is equally possible to calibrate dilution rate against hydraulic gradient, as Pollard did with the Mark II standpipe. In fact, it follows from equation (3) that the slopes of the velocity calibration lines given in Table VI may be transformed into slopes of hydraulic gradient lines by dividing each tabulated slope by the corresponding permeability. In neither case, however, will one calibration line be applicable to gravels of different permeabilities. In general, neither gradient nor velocity is the same in the standpipe and in the gravel. A qualitative,

³ Only the mean velocity in the permeameter could be determined, whereas the velocities at the individual standpoints certainly differed. Thus, the scatter of the individual measurements cannot be considered a measure of inconsistency of standpipe measurements.

2-dimensional demonstration of this is shown in Fig. 8, where K is the permeability of the gravel, and K_d the permeability of the dilution chamber. The proximity of the vertical flow lines is a measure of velocity, and the proximity of the horizontal hydraulic head lines is a measure of the hydraulic gradient.

Since no advantage accrued from the use of gradient, the calibration was performed in terms of velocity, the desired quantity in the present application.

SEALING THE DILUTION CHAMBER

From equation 21 it will be seen that the dilution rate dn/dt , is inversely proportional to the volume of the dilution chamber, v_d . It follows that the volume of the dilution chamber must be constant, and small enough so that the dilution will be accomplished in 10 to 15 minutes. For these reasons, the dilution chamber was sealed off from the upper part of the standpipe. Without this seal, the volume would vary with the stream depth. Also it would be large (300 to 1000 ml.), so that the measurements would require hours rather than minutes. Furthermore, it would be difficult to stir adequately without altering the dilution rate.

A further reason for the seal is to be found in the method of colour introduction. If colour is dropped into the open standpipe, as was done by Pollard, drops would often collect on the inner wall above water level, only to run down at a later stage and cause a serious error in the final reading of opacity number.

SPECIFIC GRAVITY OF THE COLOUR SOLUTION

Green food colour was used in the tests. It is sold in Canadian stores under the name of "Nabob Green Food Color". It is an aqueous solution of equal parts "Tartrazine and Brilliant Blue F.C.F." It has a specific gravity about 1.0264, at 20°C.

One advantage of this colour is its availability. Another, and more important advantage, is that it is not bleached by the materials with which it will come into contact. The colour used should not be a dye. Much of the scatter in Pollard's velocity data was caused by bleaching and adsorption of methylene blue. The green colour affords easy comparator readings and is sufficiently stable so that a set of standards will remain accurate for a year or more.

An approximate calculation of the hydraulic gradient across the standpipe itself will show the importance of any extraneous gradient introduced by the specific gravity of the colour solution in the dilution chamber, or by the stirring, which introduces pressure differences on different parts of the chamber walls.

Let there be a 10 cm./hr. velocity in a gravel of 100,000 cm./hr. permeability. Then the hydraulic gradient in the gravel will be 0.0001 which will be assumed to be the gradient across the standpipe.

A solution of density, ρ_1 , inside the chamber will introduce a hydraulic gradient numerically equal to the difference, $\Delta\rho$, between the densities of the solution and the water outside the chamber. If this density gradient is not to cause a dilution rate comparable with that caused by the assumed velocity, the necessary condition will be

$$\Delta\rho \ll 0.0001 \quad (22)$$

Evidently it is necessary to bring the food colour solution to the same specific gravity as the natural waters, within small limits. A solution, 16% by volume of commercial ethyl alcohol (95%) in the food colour, gives a solution of specific gravity of approximately 1.007. When 2 ml. of this solution is injected into the standpipe dilution chamber, it is diluted to 50 ml. by the water present. This results in a coloured solution of the same specific gravity as the water, because of the volume change of alcohol on dilution. The suitability of the colour is indicated by the achievement of zero dilution rate at zero velocity in all but the most permeable gravel.

A test for colour solution density may be performed in a firmly supported standpipe in a glass tank of still water, at a temperature within the range that will be encountered in the field. When 2 ml. of the colour solution is introduced and stirred once with the injector (see Appendix 2) there should be no pronounced "weeping" of colour, upward or downward, from the standpipe perforations.

ZERO ERROR

From equations (3) and (22) it will be seen that a particular specific gravity of colour solution, ρ_1 , will imply a hydraulic gradient of $\Delta\rho$, which will cause a dilution velocity proportional to the permeability, K . It has also been shown that dilution rate is proportional to velocity. Thus, the zero velocity dilution rate will be

$$\left(\frac{dn}{dt}\right) = b \Delta\rho K \quad (23)$$

where b is a constant. Furthermore, if the zero velocity dilution rate $(dn/dt)_1$, has been determined for a gravel of permeability K_1 , the zero velocity dilution rate $(dn/dt)_2$ in a gravel of permeability K_2 is

$$\left(\frac{dn}{dt}\right)_2 = \frac{K_2}{K_1} \left(\frac{dn}{dt}\right)_1 \quad (24)$$

Any observed dilution rate will include the zero velocity dilution rate as an error which will be of importance only at high permeabilities and low velocities. The rate of dilution was zero at zero velocity, in all gravels except T7, for which the zero velocity dilution rate was $3\frac{1}{2}$ numbers per hour. Since the calibration lines in Fig. 10 have all been drawn through the origin, low dilution rates measured in a gravel of permeability (K) greater than 10,000 cm./hr. should be corrected by subtracting a correction term, c , derived from equation 24,

$$c = \frac{K}{10^5} d \quad (25)$$

where d is the zero velocity dilution rate as determined in a standpipe driven into pea gravel ($K \approx 10^5$ cm./hr.) covered by still water. A 45-gallon oil drum with the top cut out and filled with clean pea gravel is adequate.

VELOCITY CALIBRATION

DILUTION RATE (dn/dt) FOR MK VI STANDPIPE VS APPARENT VELOCITY (V) FOR VARIOUS PERMEABILITIES (K)

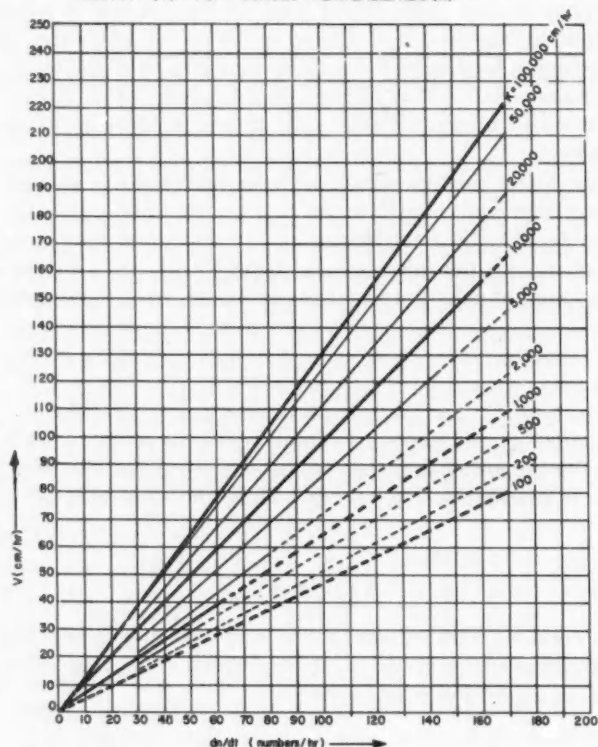


FIG. 10. Dilution rate (dn/dt) for Mark VI Groundwater Standpipe versus apparent velocity (V) for various permeabilities (K).

STIRRING

The dilution action in the standpipe was observed in a transparent replica of the dilution chamber. This chamber was inserted in gravel against one of the walls of a glass trough. A light of variable intensity was buried in the gravel behind it. When water flowed through the gravel, stratification of the water and colour solution in the chamber quickly became visible. Furthermore, it was evident that the type of stratification was dependent upon the configuration of the adjacent gravel. A slight movement of the chamber would completely change the pattern. This explained the poor correlation that Pollard found between dilution rate and apparent velocity.

It was apparent that some degree of stirring was necessary. This had to be adequate to assure uniformity of the colour solution in the chamber, yet not create an appreciable pressure gradient across the chamber, causing loss of dye.

The consensus of a long series of observations in the transparent dilution chamber was that a hook-shaped stirrer (as specified in Appendix I) rotating at 5/8 revolutions per second was satisfactory. Slower rotation (1/2 r.p.s.) allowed stratification, faster rotation (3/4 r.p.s.) allowed a measurable loss of dye by creating a pressure gradient in the standpipe. Propellor-type stirrers created vortices.

SAMPLING

The final improvement that led to consistent velocity measurement was the adoption of the "water-filled sampler" technique. While colour-alcohol mixture is being injected into the sealed dilution chamber, the water above the seal may become fairly heavily contaminated with colour. Then, if the sampler is introduced empty with the plunger depressed, the air in the shaft and sample tube becomes compressed by the water pressure so that 0.2 ml. or more of the contaminated water enters the sampler, before the needle goes through the sphincter valve into the dilution chamber. This is sufficient to cause a considerable change in the opacity number of the 2 ml. sample, particularly near the end of a series of samplings when the colour in the chamber may be as little as 0.06% of the original concentration.

Instead of using an empty sampler, 2 ml. of clean water are drawn into the sampler before it is introduced into the standpipe, and expelled just before the needle enters the sphincter valve. This flushes any contamination from the sampler.

VELOCITY CALIBRATION

The velocity measurements (rate of colour dilution) were performed immediately after each set of measurements of inflow without disturbing the standpipes. This ensured strict comparability of the permeability and velocity data. Forty-eight velocity, and 348 dilution rate determinations were made. These are summarized in Table V.

TABLE V. Summary of velocity and dilution rate measurements.

1	2	3	4	5	6	7
Gravel	No. of standpipes in permeameter	No. of velocities examined	\bar{K}	$\frac{\Delta V}{\Delta(dn/dt)}$	% P.E. in computed V	Highest velocity
			<i>cm./hr.</i>	<i>cm./No.</i>	<i>%</i>	<i>cm./hr.</i>
T5	5	12	5,150±90	0.898	4.1	134
T6	8	15	753±11	0.586	0.9	32.6
T7	8	11	98,100±1200	1.336*	1.4	391
T8	8	10	205±3	0.518	1.2	11.8

*Determined from linear portion only (below 170 Nos./hr.).

Each value of \bar{K} in column 4 is the mean of all the permeabilities observed in each gravel. These permeabilities did not need to be corrected for temperature, since velocity and permeability measurements were performed simultaneously.

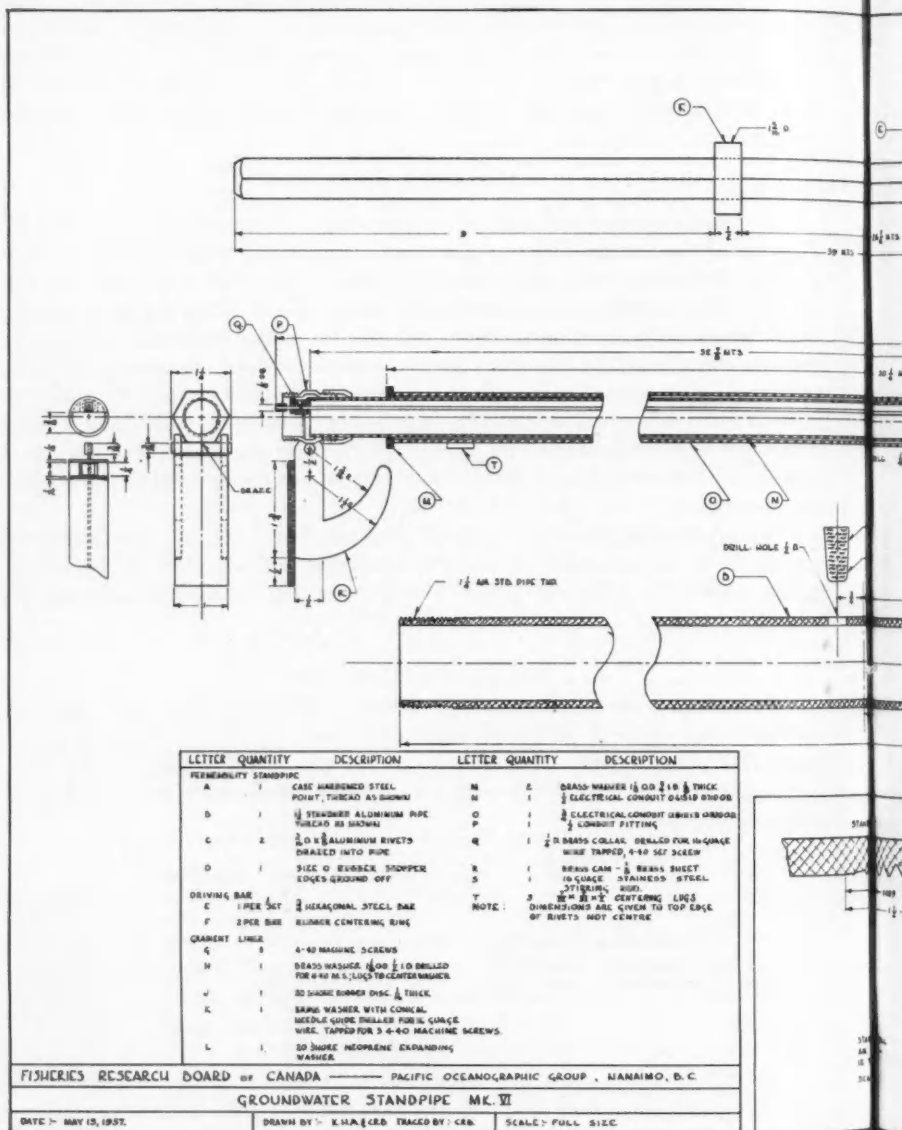
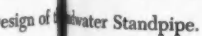


FIG. 11. Design of Groundwater Standpipe Mk. II



The zero velocity dilution rates were determined from a large number of observations of 1 hour duration.

From these zero intercepts, and the velocity and dilution rate measurements, the slopes given in column 5 were determined.

In column 6 the probable errors of apparent velocity (V) given by the calibration lines, were obtained from the percentage deviations of measured velocities, from those computed from column 4 and each dilution measurement as follows:

$$\% \text{ P.E.} = \frac{0.67}{\sqrt{N(N-1)}} \sqrt{\sum \left[100 \left(\frac{V_e - V_m}{V_e} \right) \right]^2} \quad (26)$$

where N is the number of dilution rate measurements performed, V_e is the velocity computed from dn/dt , and V_m the corresponding velocity measured in the permeameter.

Column 7 shows the highest velocities observed during calibration.

The final set of calibration data, Table VI, was obtained by graphic interpolation from the data in Table V in the following manner: the slopes in Table V were plotted against the logarithms of the corresponding permeabilities and a curve was drawn through them. From this curve, slopes of final velocity calibration lines were read off, for even values of permeability (e.g. 100, 200, 500) as shown in Figure 10. The last column in Table VI shows the velocities beyond which calibration lines must be considered extrapolations.

TABLE VI. Velocity calibration data.

K	$\frac{\Delta V}{\Delta(dn/dt)}$		V max.
	cm./hr.	cm./hr. nos./hr.	cm./hr.
100		0.475	0
200		0.515	25
500		0.581	55
1,000		0.643	64
2,000		0.719	80
5,000		0.855	145
10,000		0.988	152
20,000		1.117	159
50,000		1.250	166
100,000		1.309	170

The calibration curve for gravel T7 ($K = 98,100$ cm./hr.) was linear to about 170 numbers/hr. It curved upward, away from the dilution rate axis beyond this. It can be produced as a straight line to 200 numbers/hr. with only 7% error at this extremity. This lack of linearity at high dilution rates is undoubtedly caused by inadequacy of stirring at such high dilution rates. An increase in stirring rate would, however, cause colour loss, independent of the velocity through the gravel.

Since stirring was adequate to 170 numbers per hour in gravel T7 (220 cm./hr. velocity), extrapolation of all calibration lines to 170 numbers/hr. should be valid. Extrapolation to 220 cm./hr. would not, however, be warranted. It is

the velocity of the water in the chamber, indicated by the dilution rate, which determines the adequacy of stirring, not the velocity of the water in the gravel (see dilution theory).

ERROR

In evaluating the probable error of a field measurement of velocity, several sources of errors must be considered: those in the permeability calibration curve, those in a field determination of inflow rate, those in the velocity calibration curves, and those in the field measurement of a dilution rate. The percentage probable errors in these quantities are shown in Table VII. Only the largest of

TABLE VII. Probable errors.

Quantity	Probable error as percentage
	%
Mean permeability (calibration)	1.1
Mean inflow (calibration)	0.8
Individual inflow measurement	2.7
V computed from Figure 10 (calibration)	1.2
Individual dilution rate measurement	1.7

these, 2.7%, need be considered. Making allowance for error in plotting the permeability calibration curve, and in graphic interpolation of velocity calibration, a liberal allowance for error would be 10%. This is unimportant compared with variations in permeability and velocity that occur in nature, at points only a short distance apart.

The permeabilities and, therefore, the apparent velocities at points only a few inches apart in a river gravel differ considerably. The choice of a particular position for a measurement of permeability and velocity is largely a matter of chance. If, therefore, the method of measurement gives errors appreciably less than this variability with position, the errors have no real significance. This may be used as a criterion for the adequacy of the method of measurement.

APPLICABILITY OF CALIBRATION CURVES

The calibration curves presented in Fig. 10 are applicable to any differently-designed standpipe driven to the same depth, provided that the outer diameter, dilution chamber dimensions, and the size and pattern of perforations remain unchanged, and that the features enumerated in the conclusions are incorporated.

CONCLUSIONS

The standpipe described by Pollard (1955) was a suitable instrument for measuring low gravel permeabilities. To increase its range, and to obtain consistent velocity measurements, considerable change in design and procedure was necessary.

By the use of gravels of nearly uniform permeability which did not mask large inconsistencies in the standpipe's performance, and by various incidental experiments, it was found that:

1. To measure high permeabilities, large suction tubing is necessary.
2. To permit the use of a large suction tip without creating a vacuum in the standpipe which would disturb the one-inch head, the standpipe cannot have a narrow neck.
3. To measure velocities, methylene blue is completely unsatisfactory. A colour, not a dye, which is neither strongly adsorbed nor bleached by materials with which it comes in contact, must be used.
4. The specific gravity of the coloured solution in the dilution chamber must be made very near to that of the water at the temperature encountered.
5. The standpipe dilution chamber should be sealed during velocity measurements to lessen the volume involved and the time needed to perform a measurement; to eliminate the static column; to eliminate the effect of variation of stream depth on the volume involved; and most important, to prevent colour droplets on the walls of the standpipe from running down into the water near the end of a dilution measurement. It must be possible to insert the seal without forcing water from the perforations in the standpipe chamber.
6. A stirring mechanism must be introduced into the dilution chamber.
7. The method and rate of stirring must keep the solution in the dilution chamber uniform, but must not introduce pressure differences sufficient to cause colour loss, through the perforations in the chamber wall, independent of the apparent velocity in the gravel.
8. Some method such as the "water-filled sampler" technique must be used to avoid contamination of samples.

The Mark VI Groundwater Standpipe, which incorporates these features, will measure permeabilities ranging from 100 to 100,000 cm./hr. and apparent velocities from 5 to 200 cm./hr. with less than 10% error. This is completely adequate in view of the point-to-point variability of these quantities in nature.

The velocity calibration could be extended to 500 cm./hr. However, this is not necessary for the study of salmon spawning gravels. Wickett (1958) has shown that salmon eggs are not likely to survive when the velocity or permeability is less than the above minimum, whereas a velocity or permeability considerably less than the above maximum is adequate for survival.

ACKNOWLEDGEMENTS

The author is grateful to Mr. W. P. Wickett, who initiated this research and contributed much valuable advice, and to Dr. J. P. Tully under whose direction the work was carried out.

LIST OF SYMBOLS

V	Apparent velocity of the groundwater
V_s	Mean velocity of the water in the dilution chamber
S	Hydraulic gradient

K	Darcy's coefficient of permeability
K_T	Permeability at temperature T
Q	Volume rate of flow
A	Cross-sectional area normal to flow
T, T'	Temperatures
η	Kinematic viscosity
h	Hydraulic head
D	Depth
v	Volume
C	Concentration of colour
n	Opacity number
t	Time
L	Length in direction of flow
r	Radius
H	Depth of water
V_0	Velocity at periphery of spherical sink
r_0	Radius of spherical sink
Δh_r	Head loss to a radius r
Δh	Total head loss
W	Width of permeameter
v_d	Volume of dilution chamber
C_0	Concentration at start of dilution
e	Base of Napierian logarithms
K_d	Permeability of the dilution chamber
a, b	Constants
ρ	Specific gravity
N	Number of measurements
V_c	Computed velocity
V_m	Measured velocity
d	Zero velocity dilution rate in pea gravel
T5, T6, T7, T8	Gravels used in Calibration
c	Correction term for dilution rate
$\frac{dn}{dt}$	Dilution rate
f_v	Viscosity factor
$\left(\frac{dn}{dt}\right)_c$	Corrected dilution rate

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APPENDIX I. DESIGN OF MARK VI GROUNDWATER STANDPIPE

The Mark VI standpipe kit (Fig. 14, 15) consists of: (1) three permeability standpipes, (2) one driving bar, (3) three discs, (4) one hammer, (5) one set of suction apparatus, (6) one oxygen kit, (7) three velocity (or gradient) liners, (8) two stirring gear-motors, (9) one comparator, (10) one bottle of colour-alcohol mixture, and (11) three colour samplers.

1. PERMEABILITY STANDPIPE (Fig. 11)

The permeability standpipe consists of a $3\frac{1}{4}$ -inch length of $1\frac{1}{4}$ -inch nominal diameter aluminum standard pipe with an internal thread into which the tempered tool-steel point is fitted (a special tap is advisable). The edge of the pipe should be crimped into the groove at the lower end of the thread. Aluminum is used for lightness and for smoothness of interior. The top edges of the two diametrically opposed rivets ($1\frac{1}{16}$ inches from the top of the steel point) mark the upper end of the dilution chamber. Forty-eight $\frac{1}{8}$ -inch diameter holes, evenly spaced about the dilution chamber, allow water to flow into, or through the standpipe. Vertical grooves $\frac{1}{16}$ inch wide by $\frac{1}{16}$ inch deep in the outside of the pipe extend between the holes to reduce hole blocking by pebbles. A red band, 10 inches above the center of the dilution chamber, marks the depth to which the standpipe must be driven into gravel. A $\frac{1}{2}$ -inch hole, just above the red band, allows surface water to fill the standpipe when it is driven, to prevent high pressure inflow from the gravel from disturbing the finer particles of gravel. A pipe thread at the upper end of the standpipe allows an extension to be added if permeability measurements are to be taken through very deep water.

2. DRIVING BAR (Fig. 11)

The driving bar transmits the forces of hammer blows to the steel point of the standpipe. It is a length of $\frac{3}{4}$ -inch hexagonal steel with its lower $2\frac{1}{2}$ inches ground to $\frac{3}{4}$ -inch diameter to allow clearance for the rivets in the permeability standpipe. Rubber rings, near the ends of the bar, center it in the standpipe and lessen shock to the standpipe walls.

3. DISC (Fig. 14)

The disc lessens the slippage of surface water down the outside of the standpipe. It consists of two aluminum discs with a rubber disc between them. The discs are held together by six equally-spaced $\frac{3}{16}$ -inch diameter machine screws threaded into the lower disc. The outer diameter of the lower disc is 8 inches; that of the upper disc $3\frac{1}{2}$ inches. Each has a $2\frac{1}{2}$ -inch hole at its center. The rubber disc is $3\frac{1}{2}$ inches in diameter with a $1\frac{1}{8}$ -inch central hole.

4. HAMMER (Fig. 14)

The hammer should weigh at least 4 pounds. A heavy hammer, because it is swung more slowly, will damage the standpipes less than the sharp blow of a light hammer. Shock-absorbing hammers are available which are eminently suited to this use.

5. SUCTION ASSEMBLY (Fig. 15)

The suction gear is essentially that described by Pollard with some modifications. The suction tip is of $\frac{5}{16}$ inch O.D. copper tubing and has three thin centering lugs near its lower end. A heavy-walled rubber tube with an inner diameter of $\frac{1}{4}$ inch connects the suction tip to the brass fitting ($\frac{1}{4}$ I.D.) at the top of the 500 ml. plastic cylinder, graduated in 10 ml. intervals, which is attached to the side of the pump. The zero graduation should be placed at such a distance from the bottom of the cylinder so that the first 25 ml. of water are not recorded. A rubber stopper closes the lower end of the cylinder making it easy to empty. A smaller rubber tube leads from a ball valve at the top of the cylinder to the pump. The pump is a tire pump with a reversed piston. The pump should be capable of attaining and holding a good vacuum. The type used here will readily give a vacuum of about 27 inches of mercury. A sliding marker on the $\frac{5}{16}$ copper tubing holds the tip at any desired depth by resting on

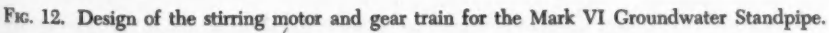


FIG. 12. Design of the stirring motor and gear train for the Mark VI Groundwater Standpipe.

top of the standpipe. Two 3-inch strips of thin, flat spring steel bolted together at the ends, with the copper tubing between them, serve adequately. They should hold the tubing firmly, yet slide on it smoothly. A one-inch spacer completes the suction gear. This is a one-inch length of 1¼-inch pipe open at one side.

6. OXYGEN KIT (Fig. 15)

The oxygen kit is the portable semi-micro Winkler kit for measuring the oxygen concentration described by Harper, 1953.

7. VELOCITY LINER (Fig. 11)

The inner tube of the liner is made from a length of ½-inch nominal diameter thin wall electrical conduit with a ¼-inch pressure equalizing hole near its lower end. A brass fitting pressed into the lower end of the conduit acts as a stop for the expanding washer, a hypodermic needle guide, and a lower stirrer bearing. A rubber disc is attached to the lower face of this fitting by means of a brass washer and three small machine screws. One small hole in the rubber disc acts as a packing gland for the stirrer. Another hole made with the hypodermic needle acts as a sphincter valve for the sampler needle. Three small lugs of the washer center the liner in the standpipe. An upper stirrer bearing of two spaced plates is brazed on the upper end of the inner liner.

The stirrer, a length of 16-gauge, stainless steel wire, with a hook at its lower end and a square shoulder brazed to its upper end, is held in position by the setscrew in a collar which turns between the plates of the upper bearing.

A ½-inch compression type conduit fitting bearing a cam is tightened onto the upper end of the inner liner. Its position can be varied to allow adjustment of the compression of the expanding washer.

The expanding washer of 20-shore neoprene, sliding on the inner liner, forms the seal between the liner and the standpipe when compressed against the conical face of the brass stop.

The outer tube of the liner transmits pressure from the cam to the expanding washer. It consists of a length of ¾-inch thin wall electrical conduit to each end of which is brazed a brass washer to provide bearing surfaces. A ¼-inch pressure equalizing hole is drilled through the outer liner near its lower end. The pressure equalizing holes reduce leakage at the sphincter valve and packing gland. Three lugs near the upper end of the outer liner center it in the standpipe. Silicone grease should be applied to the liner and brass stop under the expanding washer, and worked into the packing gland.

The effectiveness of the seals may be tested by supporting the assembled standpipe in air, starting the stirring motor, and by filling the upper portion of the standpipe with water. No leakage from the dilution chamber should be observed.

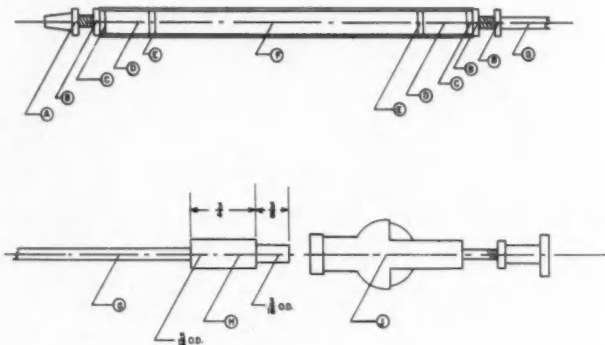
8. STIRRING GEAR-MOTOR (Fig. 12)

The 5,600 series, chronometrically governed, D.C. motors available from A. W. Haydon Company, Waterbury, Connecticut, would probably be suitable for this purpose. The motor used at present is a small 1½-volt D.C. model-boat motor—the T.K.K. Supermagnetic Motor #0 made in Japan by Tokyo Kagaku Company which retails for 89 cents. It is connected through a 5-ohm potentiometer and a switch to two size-D flashlight cells in parallel. A train of three pairs of 48 diametral-pitch gears provides a 64:1 speed reduction. The whole is enclosed in a 2½-inch square brass box, the extended lower plate of which provides a mounting, which fits over the threads of the conduit fitting at the top of the standpipe liner. The fitting nut holds the gear train firmly in place. A short length of flexible speedometer cable terminating in a square female connection which slips onto the square shoulder of the stirrer connects the gear train to the stirrer.

This gear-motor will operate the stirrer for about 8 hours continuously on one pair of flashlight cells, at sufficiently constant speed, with only half-hourly adjustment of the potentiometer. In field use, this is equivalent to at least two days work. The stirrer speed should be

SAMPLER

SCALE: 2X FULL SIZE



LETTER	QUANTITY	DESCRIPTION	LETTER	QUANTITY	DESCRIPTION
I	1	*17 HYPERDERMIC NEEDLE, END CUT SQUARE AT $1\frac{1}{2}$ INCHES (NOT SHOWN).	E	2	6-32 NUT TURNED TO $\frac{1}{8}$ O.D.
A	1	HYPERDERMIC NEEDLE FITTING WITH HEXAGONAL COLLAR AND $\frac{1}{8}$ LONG, 6-32 THREADED SHAKE CONICAL. END 0.04 MM. O.D. TO MAX. U.S. 0.300 LONG.	F	1	PYREX TUBING, 8.0MM O.D., 1.0MM WALL, $4\frac{1}{2}$ LONG.
B	3	6-32 NUT	G	1	STAINLESS STEEL TUBING, $\frac{1}{8}$ O.D., 20 BW WALL, 34 LONG.
C	2	WASHER, 1.0, $\frac{1}{8}$ O.D., $\frac{1}{8}$ THICK.	H	1	PUPETTE, FITTING BRAZED OVER (I)
D	2	RUBBER TUBING, $\frac{1}{8}$ INCH $\frac{1}{8}$ WALL.	J	1	2 ml AUTOMATIC PUPETTE.

NOTE: — ALL DIMENSIONS IN INCHES UNLESS OTHERWISE STATED.

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SAMPLER

DATE — DEC. 10, 1957

DRAWN BY — WWA

SCALE — 2X FULL SIZE.

FIG. 13. Design of sampler for the Mark VI Groundwater Standpipe.

kept at approximately $\frac{5}{8}$ revolution per second. Tests have shown that $\frac{1}{2}$ r.p.s. is too slow while $\frac{3}{4}$ r.p.s. is too fast.

This gear-motor has the following advantages: (a) it is rugged, (b) it is compact and light, even with a battery, (c) the cells are available anywhere, (d) the motor itself is expendable and easily replaced so that water damage is unimportant, (e) parts are readily available.

9. COMPARATOR (Fig. 15)

The comparator is a rack of fifteen $2\frac{3}{4}$ -inch long, $\frac{5}{16}$ -inch O.D. pyrex tubes of standard colours, spaced at 1-inch centres and numbered in half numbers from 1 to 8. Slots from the rear of the rack allow the sample tube to be brought into the same plane as that of standards. A sloping white reflector which folds flat against the rack when not in use provides even illumination.

The tubes are filled with solutions of the colour-alcohol mixture (see Colour Bottle) diluted with water to the following percentage concentrations by volume:

$$4, 4(1/\sqrt{2}), 4(\frac{1}{2}), \dots 4(\frac{1}{2})^{n-1}, \dots 4(\frac{1}{2})^7,$$

where n is the tube number in the series 1, $1\frac{1}{2}$, 2, $2\frac{1}{2}$. . . 8.

A simple method of preparing the standards follows:

- (a) To 8 ml. of colour-alcohol mixture (see Colour Bottle), add water to make 200 ml. of solution #1 and stir thoroughly.
- (b) Fill tube #1 with part of this solution.
- (c) To 50 ml. of solution #1, add water to make 100 ml. of solution #2 and stir.
- (d) Fill tube #2 with solution #2.
- (e) To 50 ml. of solution #2, add water to make 100 ml. of the next whole-numbered solution (#3) and stir, discarding the remainder of solution #2.
- (f) Fill the next whole-numbered tube (#3).
- (g) Repeat steps (e) and (f) until tube #8 is filled.
- (h) Retain the remainder of solution #8 for comparison.
- (i) To 70.7 ml. of solution #1, add water to make 100 ml. of solution #1½ and stir, discarding the remainder of solution #1.
- (j) Fill tube #1½.
- (k) To 50 ml. of solution #1½, add water to make 100 ml. of the next half-numbered solution (#2½) and stir, discarding the remainder of solution #1½.
- (l) Fill the next half-numbered tube (#2½).
- (m) Repeat steps (k) and (l) until tube #7½ is filled.
- (n) To 70.7 ml. of solution #7½ add water to make 100 ml. of solution #8.
- (o) Compare the #8 solutions from steps (h) and (n), then discard them. These solutions, in identical containers, should be indistinguishable.
- (p) Examine the numbered tubes. The gradation of colour along the rack should appear uniform.
- (q) Seal the tubes with wax.

Reliable velocity measurements with the standpipe depend upon the accurate preparation of the standards, which can be satisfactorily accomplished only by cleaning all equipment at each step and by mixing each solution thoroughly.

10. COLOUR BOTTLE (Fig. 15)

A 500 ml. bottle with a screw cap is used. The cap is attached to the neck by means of a short chain with a swivel. A simple wire hook attached to the neck of the bottle allows the bottle to be hung from the top of the standpipe to free the operator's hands.

The colour is obtained as a mixture of equal parts of "Brilliant Blue F.C.F." and "Tartrazine" dissolved in water to a specific gravity of $20^\circ/20^\circ$, 1.0264. This is commercially available as "Nabob Brand Green Food Color" from Kelly Douglas Co., Vancouver, B.C.

A solution of 16% ethyl alcohol by volume in the green food colour, having a specific gravity of approximately $15^\circ/15^\circ$, 1.007, is used in the standpipe. Because this solution is near the maximum volume contraction of alcohol and water, a volume expansion occurs when

2 ml. of the solution are added to the water in the 50 ml. dilution chamber of the standpipe. This expansion, and the algebraic dilution effect, reduce the specific gravity of the resulting solution to about 1 ± 0.00001 .

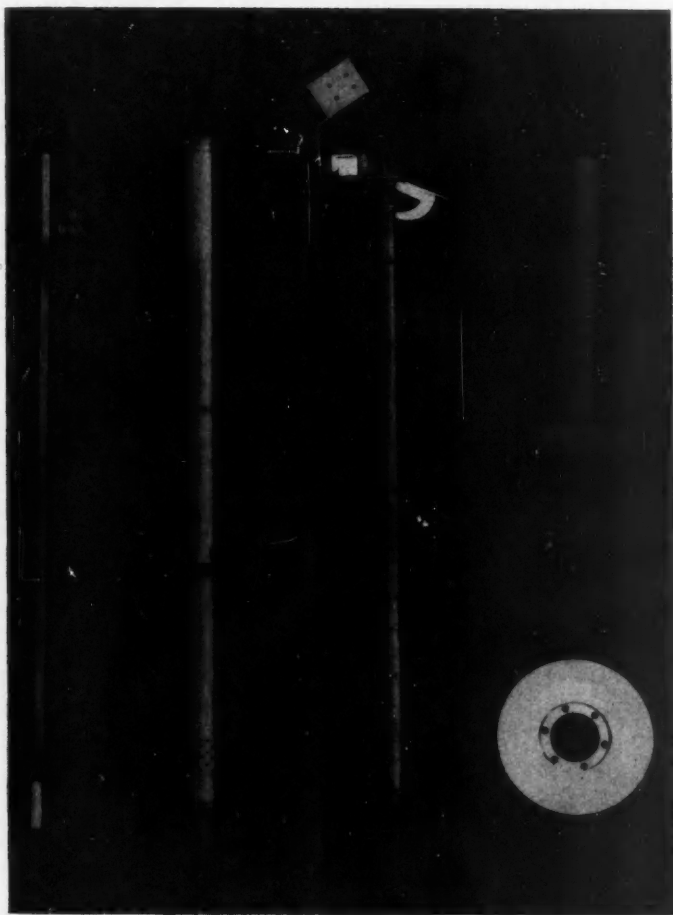


FIG. 14. The Mark VI Groundwater Standpipe, driving bar and hammer, velocity liner and disc.

If the standpipe is placed in clean pea gravel covered with still water in a trough or 45-gallon drum, the stirrer placed in operation, and colour introduced, a dilution rate of not more than $3\frac{1}{2}$ numbers per hour may be considered as evidence that the specific gravity of the colour is adequately adjusted and that the stirrer is not causing excessive colour loss.

The dilution rate obtained should be recorded for the colour-alcohol batch being prepared for use in correcting dilution rates.

11. COLOUR SAMPLER (Fig. 13)

Three samplers are provided, so that one may be used as a colour injector and one as a sampler, while the third is carried as a spare. Extra needles and sample tubes are desirable.

The sampler consists of a syringe, an extension tube, a sample tube and a needle. The syringe is a 2 ml. automatic pipette adjusted so that when the plunger is depressed without too great effort *metal to metal contact is obtained*. The extension tube is a 32-inch length of 20 B.W. gauge, $\frac{1}{8}$ -inch O.D. stainless steel tube with a male pipette fitting brazed to its upper end to connect to the syringe, and the tube fitting shown in Fig. 13 brazed to its lower end.

The sample tube is a 4½-inch length of $\frac{5}{16}$ O.D. pyrex tubing identical to that used in the comparator tubes. A special fitting shown in Fig. 13 connects the tube to the hypodermic needle.

The needles are 2-inch #17 hypodermic needles cut off square at $1\frac{1}{4}$ inches and rounded at the tips.

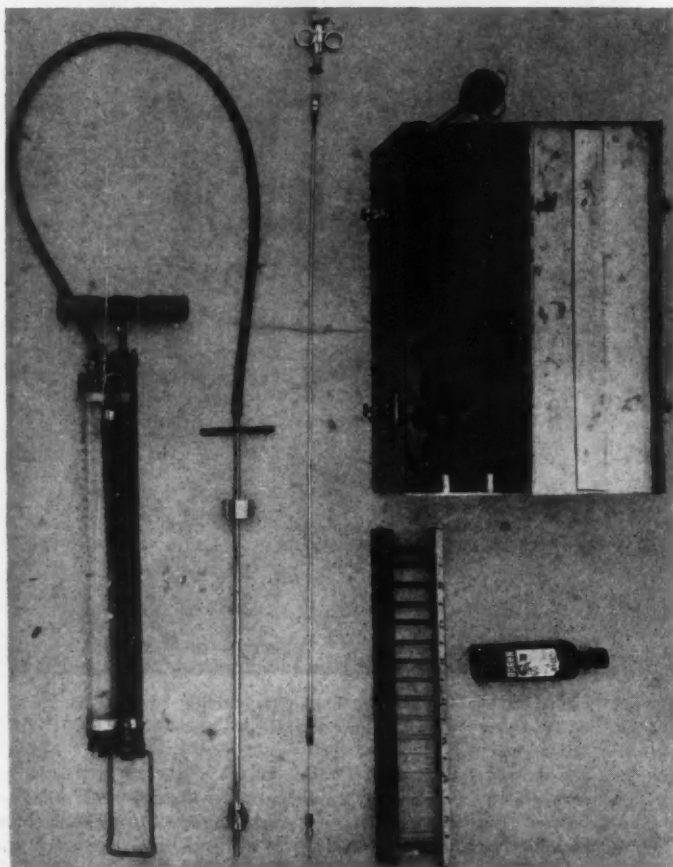


FIG. 15. The pump, syringe, and oxygen analysis kit for use with the Mark VI Groundwater Standpipe.

APPENDIX II. PROCEDURE FOR USE OF MARK VI GROUNDWATER STANDPIPE

1. DRIVING THE STANDPIPE

Remove the liner from the standpipe and remove the rubber stopper from the hole in the standpipe wall. Carefully place the driving bar in the standpipe with the cylindrical end down. By means of axial blows on the bar, drive the standpipe until the red line is flush with the surface of the gravel. Oblique blows, which will shorten the life of the standpipe and cause lateral movement of the pipe, must be avoided. If the standpipe encounters a large rock and is deflected sideways, especially when nearly completely driven, the hole made in the gravel will be enlarged and erroneously high values of permeability will be obtained. If lateral movement is suspected, it is advisable to move to a new, nearby location.

Now replace the rubber stopper. Next scrape away the top inch of gravel from an 8-inch circle around the standpipe and replace it by the finest sand or gravel at hand, which will neither wash away nor sift down through the gravel. Then slip the aluminum disc over the standpipe, press it down firmly, and cover it with fine sand or gravel. The purpose of this disc is to lessen the slippage of water down the sides of the standpipe to the chamber during permeability measurements. Its omission will lead to occasional erroneously high permeability values, especially when the standpipe has moved laterally during driving.

2. MEASUREMENT OF PERMEABILITY

Two men are required, one to pump while the other manipulates the suction tip and stopwatch. Place the 1-inch spacer on top of standpipe. Introduce the copper suction tube into the standpipe so that its tip is slightly above the water level while the sliding marker rests across the top of the spacer. Start pumping. Slowly and carefully slide the suction tip downward until it touches the water surface. This point is indicated by a "slurping" sound. The first "slurp" should be used as the surface indication. Stop pumping. Remove the spacer and lower the suction tube till the marker rests on top of the standpipe without allowing the marker to move on the tube. Empty the water receiver.

Pinch off the rubber tube and, by several quick pump strokes, obtain a full vacuum. Continue pumping furiously. Simultaneously, release the rubber tube and start the stopwatch. Before the receiver overflows, simultaneously stop the watch and raise the suction tip out of the water. Stop pumping. Record the time interval and the volume of water collected as indicated by the graduations on the water receiver. Measure and record the temperature of the water inside the standpipe.

The first 25 ml. of water, which had to be removed from the standpipe to reduce the water level by 1 inch, will have been subtracted by the positioning of the zero graduation described with the suction assembly. The time required to remove this 25 ml. should be subtracted from the recorded time interval. This time correction can be determined for the particular suction apparatus by repeated measurements of suction rate with the suction tip in open water. From this corrected volume and time, calculate the inflow, Q , in ml./sec. and read the permeability, K_p , at the observed temperature from the calibration curve (Fig. 5).

If it is desired, permeabilities may be reduced to 10°C., for comparison of gravels whose permeabilities were measured at different temperatures, by the following equation:

$$K_{10} = f_v K_T$$

where f_v , the viscosity factor, equals the kinematic viscosity at $T^\circ\text{C.}$ divided by the kinematic viscosity at 10°C. Do not make this correction to the inflow rate, Q .

Viscosity factors for observed temperatures from 0° to 24°C. are given graphically in Fig. 6.

By starting with a full vacuum, the suction tip quickly lowers the water level inside the pipe by 1 inch and then, by alternately sucking air and water, maintains that level. Removal of the tip from the water at the end of the timed interval allows water in the tubing to reach

the receiver but prevents residual vacuum in the receiver from withdrawing more water from the standpipe.

Unless a sucking sound is heard throughout the timed interval, the pump is not removing water fast enough to maintain the 1-inch head. In this case it can only be said that the permeability is higher than the value indicated by the pumping rate.

3. REMOVAL OF TURBIDITY

With the suction tube still set for a 1-inch head, very slowly pump water from the standpipe, emptying the receiver as necessary, to remove turbidity. At least 500 ml. of water should be removed to ensure removal of surface water.

4. MEASUREMENT OF DISSOLVED OXYGEN

When the turbidity and all surface water has been removed slowly, a sample of water, about 25 ml., is withdrawn from the lower part of the standpipe very gently so that oxygen is not removed from the water by a sharp pressure drop. The dissolved oxygen concentration in milligrams per litre is determined by the abridged Winkler method (Harper, 1953) with a portable kit.

Wickett has found that with the Mark I standpipe, slightly higher oxygen values were obtained immediately after driving the standpipe than those obtained after the standpipe had been allowed to remain in the gravel for a few days. This was probably caused by slippage of surface water down the sides of the standpipe in the freshly disturbed gravel which later compacted around the standpipe. If the present standpipe does not move laterally, and if the discs are used, this effect should be eliminated.

5. MEASUREMENT OF VELOCITY

First check the stirrer to make sure that it turns fairly easily and, if necessary, work a little silicone grease into the rubber packing. Then, with the expanding washer relaxed, slowly lower the liner into the standpipe. Depress the cam to seal the dilution chamber. Attach and start the stirring motor. Adjust its speed until the stirrer rotates 5 times in 8 seconds—a mark on the flexible drive will help. Hang the open colour bottle from the top of the standpipe. Have two assembled samplers at hand, one of which will be referred to hereafter as the colour injector, and should be used for that purpose only. The other should be used as a sampler only.

With the injector, withdraw 2 ml. of the colour-alcohol mixture from the bottle. The only importance of the quantity is that it ensures a start point at, or not much lighter than, the darkest tube in the comparator, thus permitting maximum difference of dilution number and, therefore, greatest accuracy. Lower the injector into the liner as far as it will go. It is easy to tell when it has entered the sphincter valve by the resistance felt. Depress the pipette plunger and hold it depressed for 2 or 3 seconds. Withdraw the plunger, pause, then depress it again. With the plunger depressed, withdraw the empty injector from the liner. Withdrawing and depressing the plunger assures a thoroughly mixed solution at the start of the run.

As quickly as possible, withdraw a sample from the dilution chamber in the following manner: Draw 2 ml. of clean water into the clean sampler. Lower it into the liner until it touches the sphincter valve, raise it slightly, then depress the plunger expelling the water. Pause 2 or 3 seconds, and then, with the plunger still depressed, push the needle through the sphincter valve as far as it will go. Withdraw the plunger and start the stopwatch. Pause 3 or 4 seconds, then, with the plunger still withdrawn, remove the filled sampler from the liner. Turn the needle end of the sampler uppermost and compare the sample with the standards in the comparator. Record the dilution number to the nearest quarter number. Wash the sampler thoroughly and draw 2 ml. of clean water into it.

Shortly before the stopwatch reaches the 5-minute mark, lower the water-filled sampler into the liner and make sure the sphincter valve is located. About 5 to 10 seconds before the 5-minute mark is reached, expel the water and, keeping the plunger depressed, push the needle firmly into the dilution chamber.

When the stopwatch indicates 5 minutes, withdraw the plunger, pause 3 or 4 seconds and withdraw the filled sampler from the standpipe. Read the dilution number from the comparator and record it to the nearest quarter number. Wash the sampler thoroughly and fill with 2 ml. of clean water. Then proceed according to the following table:

<i>Change in dilution number in 5 minutes</i>	<i>Proceed as below</i>
Less than $\frac{1}{2}$	3rd sample at 60 minutes
$\frac{1}{2}$ to 1	" " " 30 "
1 to 2	" " " 15 "
2 to 3	" " " 10 "
3 to 4	" " " 7 "
4 to 5	" " " 7 "
Over 5	No further sample, but repeat whole procedure.
2nd sample paler than #8	Repeat procedure taking 2nd sample at 3 minutes, and repeat.
2nd sample at 3 minutes paler than #8	Repeat procedure with minimum possible time between injection and taking of first sample. Take 2nd sample at less than 3 minutes (e.g., 2 minutes) and repeat. Greater speed in sampling may be obtained by using 2 men and 2 samplers.

If it was possible to obtain three samples, calculate hourly dilution rate from the first and second samples, and from the first and third samples.

If only two samples could be obtained and, therefore, the run was repeated, calculate the hourly rate for each run.

Compare the hourly rates. If they differ by more than about 10%, the whole procedure should be repeated. If they agree well enough, use the hourly rate obtained from the longest time period observed to minimize percentage error. From the graph of velocity versus dilution rate (Fig. 10) read the apparent velocity. A table of dilution numbers in 1, 2, 3, 4, 5, 7, 10, 15 and 30 minutes with conversion to hourly rates is an excellent aid to field crews.

The tabulated times for third samples need not be exactly adhered to. They are only proposed as a guide to obtain as large a spread as possible between first and third samples to minimize the importance of errors in estimation of dilution numbers.

If the permeability, K , of the gravel is between 10,000 and 100,000 cm./hr. a correction for zero velocity dilution rate should be made to the dilution rates obtained, before using the velocity calibration curve. If the zero velocity dilution rate in pea gravel for the colour-alcohol batch in use is " d " numbers per hour (see "colour bottle", Appendix I), and a measured dilution rate is dn/dt numbers per hour, then the corrected dilution rate, $(dn/dt)_c$, is given by:

$$\left(\frac{dn}{dt}\right)_c = \frac{dn}{dt} - d \cdot \frac{K}{10^5}$$

This is important only at low velocities and high permeabilities.

The importance of a clean sampler, especially when the sample is very dilute, cannot be over-emphasized. The ratio of concentration of colour #1 to colour #8 is 128:1. If 0.1 ml. of colour #1 is accidentally picked up with a 2 ml. sample of #8 colour the reading obtained will be #6 $\frac{1}{2}$! This is the reason for filling the sampler with water and expelling it just above the sphincter valve.

Detailed drawings of the Mark VI Standpipe and the Stirring Motor and Gear Train are available on application to

Fisheries Research Board of Canada,
Pacific Oceanographic Group,
Nanaimo, B.C.

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Drift Bottle Observations in the Strait of Georgia¹

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ABSTRACT

Drift bottle observations were carried out in the Strait of Georgia during the summers of 1926-1929. A total of 1,636 bottles was released of which 672 were recovered, giving an over-all return of 41%.

No consistent pattern of drift in the strait as a whole could be clearly drawn from the recoveries. Some consistency of circulation in local areas can be inferred from the net drift of bottles.

Winds dominated drift bottle movements in the open strait, where tidal currents are weak. A general northwestward drift was noted from releases along the eastern side of the strait and a southeastward drift along the western side. This suggests a large counterclockwise circulation of surface water over the whole strait. A smaller gyral circulating in the same direction is apparent in the southern strait, south of a line from Sand Heads to Active Pass.

A strong surface current is directed from the Fraser River estuary across the strait to the passes among the Gulf Islands. This seaward flow of fresh water is augmented by a strong seaward tidal current during large ebb tides.

Tidal currents are strong with definite periodicities in the channels bordering the strait. Current speeds of more than 26 cm./sec. (0.5 knot) were calculated from data on drift bottles whose drift was of brief duration. Average speed of drift was about 10 cm./sec. (0.2 knot).

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INTRODUCTION

AS PART OF A GENERAL PROGRAM to study the inshore marine environment associated with the fisheries on the British Columbia coast, extensive series of

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drift bottle experiments were conducted by earlier investigators at this station during the summers of 1926 to 1929 inclusive. The immediate objective of the experiments was to determine the surface circulation in the Strait of Georgia. Movements of Fraser River water with reference to the marine movements of salmon, particularly sockeye salmon, were of special interest.

With the exception of three series of 1927 drift bottle observations studied and reported previously (Waldichuk and Tabata, 1955; Waldichuk, 1957, pp. 387-9), results of these early experiments have remained unpublished. In the interests of providing further elucidation on the circulation in the Strait of Georgia, many of the data are being submitted here with distribution charts of the principal series of drift bottle releases and recoveries. The results have practical interest in such problems as pollution along the shores of the strait.

METHOD

Drift bottles were released during the course of other oceanographic observations. The C.G.M.S. *A. P. Knight*, a vessel of the Biological Board of Canada, was engaged in most of this early oceanographic work.

Various types of commercial bottles were used, but ketchup and "Coca Cola" bottles were most popular. The bottles were ballasted with sand so that they would float with only a minimum of surface exposed to the direct effect of the wind. Inserted in each bottle was a self-addressed and stamped card bearing a serial number and instructions to the finder to fill in information on recovery place and date and return to the Director of the Pacific Biological Station at Nanaimo. As incentive to increase returns, a small monetary reward (25 cents) was offered to the finder of each bottle. To keep them water tight, bottles were corked and sealed with marine glue. Most bottles used in these experiments had no drags attached, so that they responded almost entirely to the movement of a thin surface layer of water, and were little affected by wind.

Bottles were liberated singly from the stern of the ship at set time intervals as it followed a straight course at constant speed. Consequently, they were evenly distributed, generally spaced at about 200-yard intervals, when released on a given line. In some of the later series of 1929, bottles were released in groups at various points. To determine the change in drift with the change in tide in some of the channels, bottles were released singly at regular time intervals throughout a tidal cycle.

Because there is always some question of whether the drift of drag-free bottles is comparable to the drift of bottles with drags attached, an experiment was carried out in 1931 to provide the answer. Bottles were liberated in pairs, each pair consisting of one bottle with a drag and one without, on a run between Point Grey and Entrance Island, during a short ebb tide on 12 June. Wind was easterly of moderate strength. The first pair was liberated $2\frac{1}{2}$ miles WSW of Point Grey, the last bottle 1 mile north of Entrance Island. The time interval between releases of consecutive pairs of bottles was 5 minutes and the speed of the ship was 8 knots.

RESULTS FROM DRIFT BOTTLE RECOVERIES

A summary of the drift bottle experiments with numbers of bottles released and recovered is given in Table I.²

A total of 1,636 bottles was released during the four summers of 1926-1929. Of these, 672 bottles were recovered and cards returned, an over-all recovery of 41.1%. The distributions of drift bottle recoveries are given in Fig. 1-25. Rather than deal with the results of the drift bottle experiments according to area, the various series have been described in chronological order. All charts of drift bottle recovery distributions show curves for the summer discharge of the Fraser River, northwest and southeast components of the winds at Vancouver during and about a month following drift bottle releases, and tides for Point Atkinson for several cycles following release of bottles.

While it can only be conjectured how the bottles moved from the time they were released to the time they were recovered, an attempt has been made to plot a realistic trajectory for every series of bottles. Generally a course of drift has been deduced from the recoveries which follow one another at reasonable time intervals. For example, in choosing a trajectory from a point on the east side of the Strait of Georgia to a point on the west side around the north end of Texada Island, the reasoning has been used that bottles drift along the shores where adjacent bottles from the same series landed. The pattern of drift in open waters, in some cases, has been drawn to conform to the circulation derived from a study of the dynamics (Waldichuk, 1957, pp. 404-14).

1926 SERIES

Drift bottle releases during the summer of 1926 were concentrated in the southern part of the Strait of Georgia with emphasis on lines N-S across the Fraser River estuary and on a line E-W from Point Grey to Entrance Island. In all, 6 releases totalling 490 bottles were made during the period 6 to 13 August. Recoveries totalled 104 bottles, a return of 21.2%. The recoveries and suggested pattern of drift are given in Fig. 1-5 for all but one series, which had only 3 returns.

Winds were somewhat variable during the period when releases were made, with fairly strong northwest winds during 6 to 7 August, moderate southeast winds on 8 August, followed by 3 days of moderate northwest winds. Bottles released in the first series across the Fraser River estuary (Fig. 1) on 6 August were apparently dominated by the northwest wind and drifted into the southern part of the Strait of Georgia after having moved into the middle of the strait from the Fraser River estuary. It is noteworthy that some of the bottles drifted into Burrard Inlet and Boundary Bay. Two bottles drifted into the open Pacific, one of these landing at Amphitrite Point, B.C., and the other at Haystack Rock, Oregon.

² More complete data on releases and recoveries are available in the form of a Manuscript Report (Oceanographic and Limnological Series).

TABLE I. Summary of drift bottle experiments, 1926-1931.

Series	Bottle numbers	Released		Date	Release area	No. released	No. recovered	Percentage recovery
		Time						
26.1	1-110	1850-2030		6 Aug. '26	Sand Heads Lightship to Pt. Grey	110	18	16.4
26.2	111-250	1245-1535		7 Aug. '26	Pt. Grey to Entrance Is.	140	19	13.6
26.3	251-265	1000-1130		12 Aug. '26	Sand Heads Lightship to Pt. Roberts	99	23	23.2
26.4	266-295	1815-1840		12 Aug. '26	North of Lummi Is. to Sucia Is.	30	3	10.0
26.5	380-420	0635-0715		13 Aug. '26	Sucia Is. to East Pt., Saturna Is.	41	17	41.5
26.6	421-490	0825-0915		13 Aug. '26	East Pt., Saturna Is., to Pelorus Pt., Moresby Is.	70	24	34.3
Total for 1926						490	104	21.2
27.1	501-590	0852-1142		4 July '27	Entrance Is. to Pt. Grey	90	51	56.7
27.2	591-623	1625-1755		25 July '27	On line N-S in mid Haro Str.	33	15	42.4
27.3	624-660	0955-1143		26 July '27	On line S-N in mid Rosario Str.	37	18	48.7
27.4	661-704	1430-1557		26 July '27	Pt. Roberts to Sand Heads Lightship	44	27	61.4
27.5	705-739	1608-1651		26 July '27	Sand Heads Lightship to Bowen Island	35	23	65.7
27.6	740-825	1700-1925		26 July '27	Pt. Grey to Entrance Is.	86	48	55.8
27.7	826-874	1315-1549		30 July '27	Active Pass to Sand Heads Lightship	49	28	57.1
27.8	875-938	1148-1418		4 Aug. '27	Entrance Is. to Pt. Grey	64	34	54.7
Total for 1927						438	244	55.7
28.1	939-985	1133-1307		23 May '28	Portier Pass to Sand Heads Lightship	47	24	51.1
28.2	986-1000	1307-1430		23 May '28	Sand Heads Lightship to Pt. Roberts	42	20	47.6
28.3	1404-1430	1430-1530		23 May '28	Pt. Roberts to Active Pass	27	14	51.9
28.4	1431-1467	(1800-2100)*		6 July '28	Pt. Grey to Entrance Is.	37	19	51.4
28.5	1468-1511	1030		25 July '28	Village Bay, Mayne Is.	44	26	59.1
28.6	1512-1514	-0730		-26 July '28	Narvaez Bay, Saturna Is.	14	6	42.9
28.6	1515-1525	1030-1130		26 July '28				
28.7	1526-1532	1930		26 July '28				
28.7	1533-1539	-1230		-27 July '28				
28.7	1539-1559	0830		27 July '28	In Boundary Pass, midway between Saturna Is. and Waldron Is.	7	5	71.4
28.8	1540-1614	0930		27 July '28	In channel between Sucia Is. and Matia Is.	7	4	57.1
28.9	1615-1639	0725-1340		28 July '28	Sucia Is. to Sand Heads Lightship to Entrance Is.	75	28	37.3
28.9		1100-1615		6 Aug. '28	From point 3 mi. S. of Winchelsea Is. to N. end Texada Is.	25	13	52.0
28.10	1640-1649	1730-1900		6 Aug. '28	N. end Texada Is. to NE. side Savary Is.	10	3	30.0
28.10	1650-1668	0940-1110		7 Aug. '28	Tongue Pt., Hernando Is., to Quathiaski Cove, Quadra Is.	19	8	42.1
28.11	1669-1688	0920-1050		8 Aug. '28	Quathiaski Cove to Plumper Bay on Discovery Passage	20	6	30.0
28.12	1689-1700	0940		9 Aug. '28	Johnstone Str. opposite entrance to Okisollo Channel	12	5	41.7
28.12	1701-1705	1000		9 Aug. '28	In Okisollo Channel midway from Johnstone Str. to O'Hollos Bay	5	1	20.0
28.13	1716-1720	1478		9 Aug. '28	Calm Channel opposite Deer Pass	5	2	40.0
28.13	1721-1725	1435		9 Aug. '28				

28.12	1680-1700	0940	9 Aug. '28	Johnstone Str opposite entrance to Okisollo Channel	12	5	1	20.0	41.7
	1701-1705	1000	9 Aug. '28	In Okisollo Channel midway from Johnstone Str.	5				
28.13	1721-1725	1415	9 Aug. '28	Channel between Johnstone and Cape Mudge	5	2		30.0	
	1726-1730	1435	9 Aug. '28	Channel between Cape Mudge and Cape Lazo	5			20.0	
	1731-1735	1445	9 Aug. '28	Calm Channel just S. of Deer Passage	5	5	4	80.0	
		1715	9 Aug. '28	1 m. N. of Mitenatch Is., in northern Str. of Georgia	5	3		60.0	
28.14	1736-1740	1935	9 Aug. '28	3 mi. E. of Cape Lazo, in Str. of Georgia	5	3		60.0	
	1741-1744	1230	10 Aug. '28	4 mi. E. of Cape Lazo	4	1		25.0	
	1745-1749	1430	10 Aug. '28	Off Yellow Rock Lt., Denman Is.	5	2		40.0	
28.15	1750-1754	0725	11 Aug. '28	3 mi. off Qualicum	5	5	2	40.0	
	1755-1759	0825	11 Aug. '28	3 mi. off Parksville on line with S. end Texada Is.	5	2		40.0	
	1760-1765	0900	11 Aug. '28	1 mi. N. of Ballenas Is.	6	1		16.7	
	1766-1770	0930	11 Aug. '28	Midway between Ballenas Is. and Winchelsea Is.	5	3		60.0	
	1771-1775	0950	11 Aug. '28	1 mi. S. of Winchelsea Is.	5	5	3	60.0	
	1776-1780	1010	11 Aug. '28	1 mi. N.E. of Piper's Lagoon, near Hammond Bay	5	3		60.0	
Total for 1928									45.7
29.1	1800-1812	1545-1645	9 Aug. '29	Kulushan Pt. to Cape Mudge	13	8		61.5	
	1813-1826	1830-1930	9 Aug. '29	Cape Mudge to Quathiaski Cove	14	7		50.0	
29.2	1827-1837	0730-0830	10 Aug. '29	Quathiaski Cove to Seymour Narrows	11	3		27.3	
	1838-1845	0845-0930	10 Aug. '29	Seymour Narrows to Okisollo Chan.	8	2		25.0	
29.3a	1846-1863	0900-0915	16 Aug. '29	2 mi. S. of Gabriola Pass in Str. of Georgia	18	6		33.3	
	1864-1883	1000-1015	16 Aug. '29	Opposite Porlier Pass in Str. of Georgia	20	8		40.0	
	1884-1899	1145-1200	16 Aug. '29	Off Active Pass in Str. of Georgia	16	7		43.8	
29.3b	1900-1908	1223-1240	16 Aug. '29	Off Boat Pass in Str. of Georgia	9	5		55.6	
	1909-1919	1300-1310	16 Aug. '29	Boundary Pass, between Fatos Is. and Saturna Is.	11	7		63.6	
	1920-1927	1330-1335	16 Aug. '29	SW. of Sandy Pt., Waldron Is.	8	2		25.0	
29.4	1928-1938	1220-1222	17 Aug. '29	1 mi. W. of Sandy Pt., Waldron Is. (S. of tide rip in Boundary Pass)	11	4		36.4	
	1939-1948	1230-1232	17 Aug. '29	1½ mi. SE. of East Point, Saturna Is. (N. of tide rip in Boundary Pass)	10	4		40.0	
	1949-1966	1240-1242	17 Aug. '29	1 mi. E. of East Pt.	18	10		55.6	
29.5	1967-1975	1250-1252	17 Aug. '29	1½ mi. N. of East Pt.	9	7		77.8	
	1976-1985	1430-1437	17 Aug. '29	2½ mi. E. of Active Pass on line with Pt. Roberts	10	8		80.0	
	1986-1999	1535-1540	17 Aug. '29	3 mi. NE. of Active Pass	14	7		50.0	
	2000-2005	1710-1715	17 Aug. '29	3 mi. NE. of Porlier Pass	6	3		50.0	
	2050-2060	1730-1800	17 Aug. '29	Off Porlier Pass in Str. of Georgia	11	1		9.1	
	2061-2071	1815-1818	17 Aug. '29	Off Flat Top Islands, near SE. end Gabriola Is.	11	7		63.6	
	2072-2085	1915-1920	17 Aug. '29	At entrance to Nanaimo Hr. near Snake Is. bell buoy	14	5		35.7	
Total for 1929									45.9
31.1	2004-2049	1715-1935	12 June '31	Pt. Grey to Entrance Is.	55	18		32.7	
	2053								
	1783-1787								
	1790, 1793								
	1797								
Grand total									40.8

*Estimated.

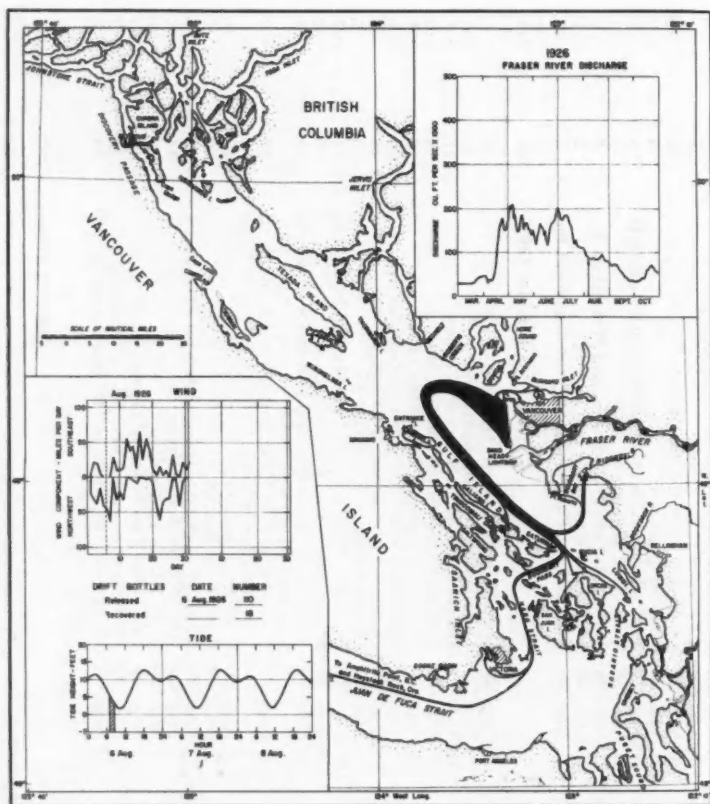


FIG. 1. Distribution of recoveries of drift bottles, Series 26.1, released on a line from Sand Heads Lightship to Point Grey, August 6, 1926. (Hatched section on tide curve, dotted line on wind diagram, and solid arrow on Fraser River hydrograph indicate period of drift bottle release. Numbers at arrowheads of drift patterns indicate how many bottles recovered.)

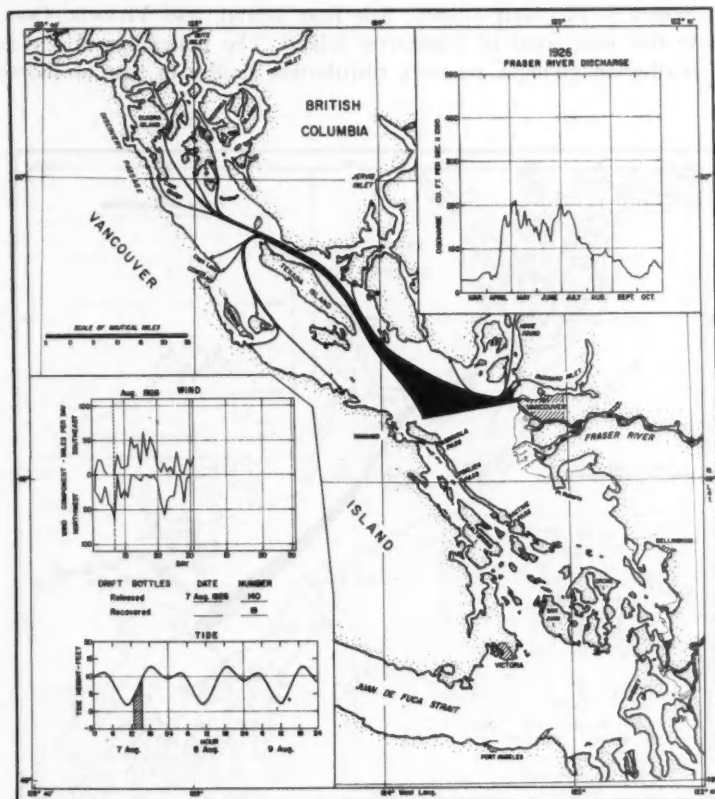


FIG. 2. Distribution of recoveries of drift bottles, Series 26.2, released on a line from Point Grey to Entrance Island, August 7, 1926.

The second series of drift bottles released 7 August across the Strait of Georgia showed a reversal in the direction of movement (Fig. 2) from those of the previous day. Bottles drifted predominantly northward, with some drifting into Burrard Inlet and Howe Sound, but the majority landing on islands at the northern end of the strait and near Cape Lazo. The last bottle liberated in this series near Entrance Island actually drifted across the strait and landed at Britannia Beach in Howe Sound. It is presumed that, while there was a fairly strong northwest wind on the day the bottles were released, the wind shifted to southeast on the following day, moving the bottles, which were still afloat, northward.

In Fig. 3 is shown the drift of bottles which occurred following a release across the southern part of the Fraser River estuary during southeast winds. At least five bottles from this series drifted toward Active Pass and were recovered at

various points in the Gulf Islands, San Juan Island, and Victoria. One even drifted to the west coast of Vancouver Island. The remainder of the bottles drifted northward giving a recovery distribution similar to that of the second series.

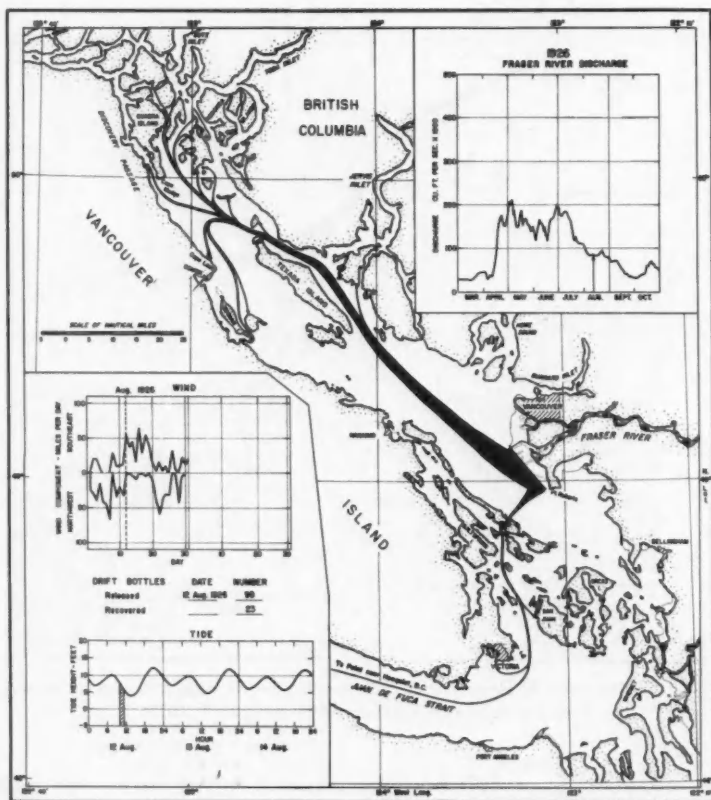


FIG. 3. Distribution of recoveries of drift bottles, Series 26.3, released on a line from Sand Heads Lightship to Point Roberts, August 12, 1926.

Figures 4 and 5 illustrate the movement of drift bottles southward from the Boundary Pass area between Saturna and Sucia Islands. Since the bottles in both these series were liberated during approximately the beginning of the ebb tide, strong tidal currents probably carried the bottles southward for a considerable distance immediately following release. Subsequent southward movement probably resulted from the net seaward flow of surface water through Haro Strait.

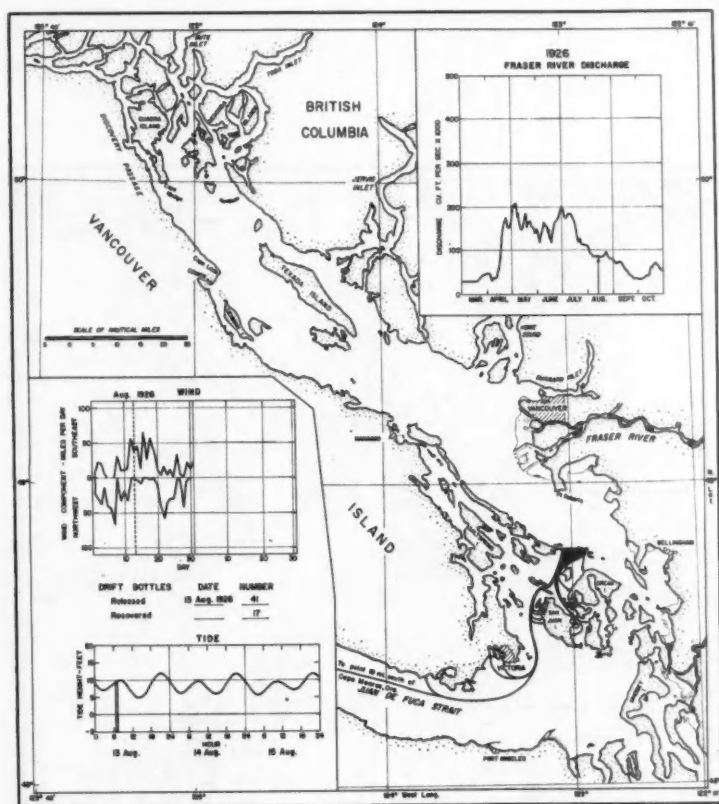


FIG. 4. Distribution of recoveries of drift bottles, Series 26.5, released on a line from Sucia Island to East Point, Saturna Island, August 13, 1926.

1927 SERIES

There were 8 series with a total of 438 drift bottles released in the Strait of Georgia during the months of July and August. Of these, 244 bottles were recovered and cards returned giving the remarkably high recovery of 55.7%. Lines of release were confined to the southern part of the strait including the line from Point Grey to Entrance Island.

Series 27.1 (Fig. 6) was released on a line from Entrance Island to Point Grey during a period of southeast winds. The majority of the bottles drifted northward. A number of bottles released near the western end of the line drifted southward, however. It is probable that the predominance of a southeast wind for about 12 days following release was responsible for the dominant

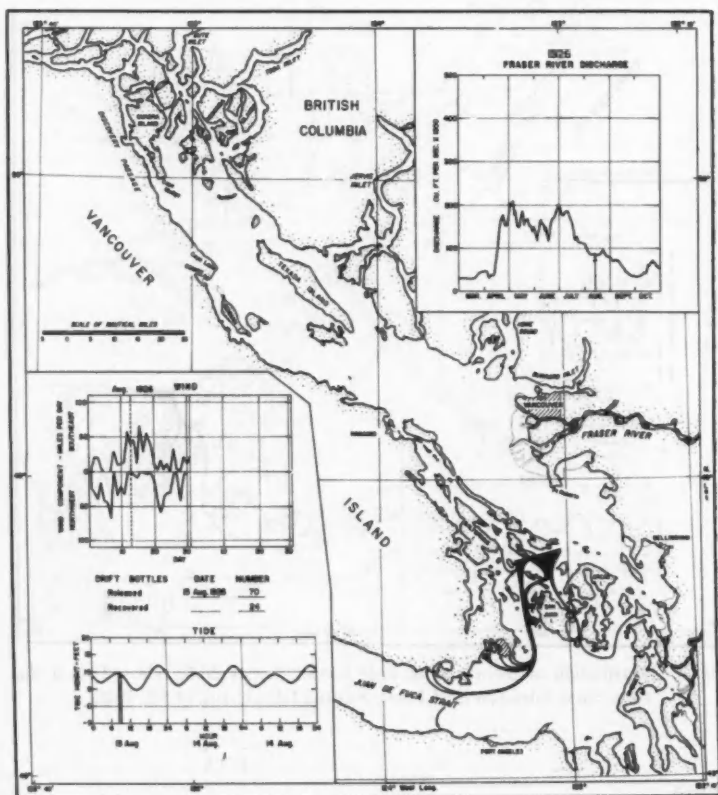


FIG. 5. Distribution of recoveries of drift bottles, Series 26.6, released on a line from East Point, Saturna Island, to Pelorus Point, Moresby Island, August 13, 1926.

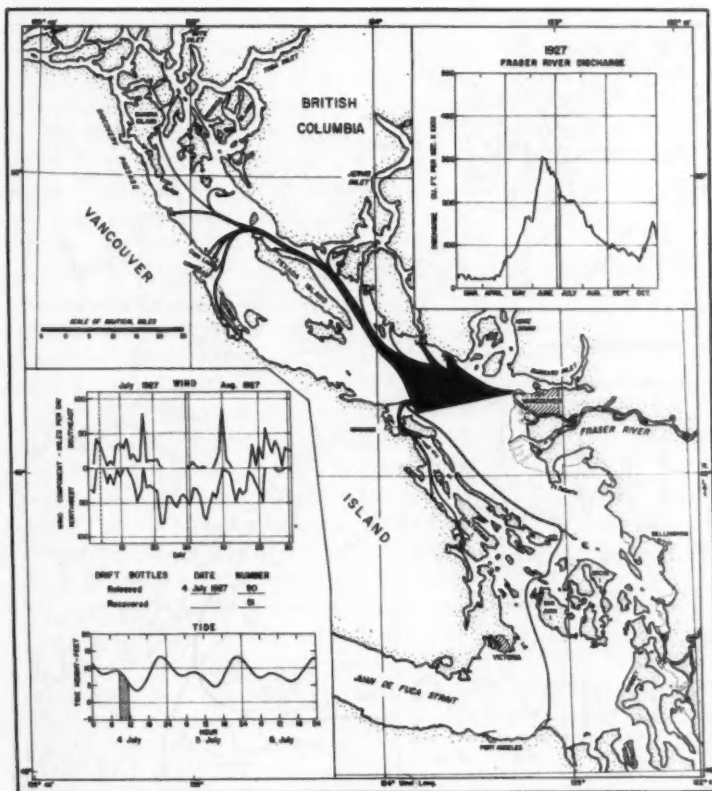


FIG. 6. Distribution of recoveries of drift bottles, Series 27.1, released on a line from Entrance Island to Point Grey, July 4, 1927.

northward drift of the bottles. A very large proportion of the bottles in this series landed at Roberts Creek, just northwest of Howe Sound. A strong onshore component of the winds in the area coupled with inshore movement of Fraser River water was probably responsible for this drift.

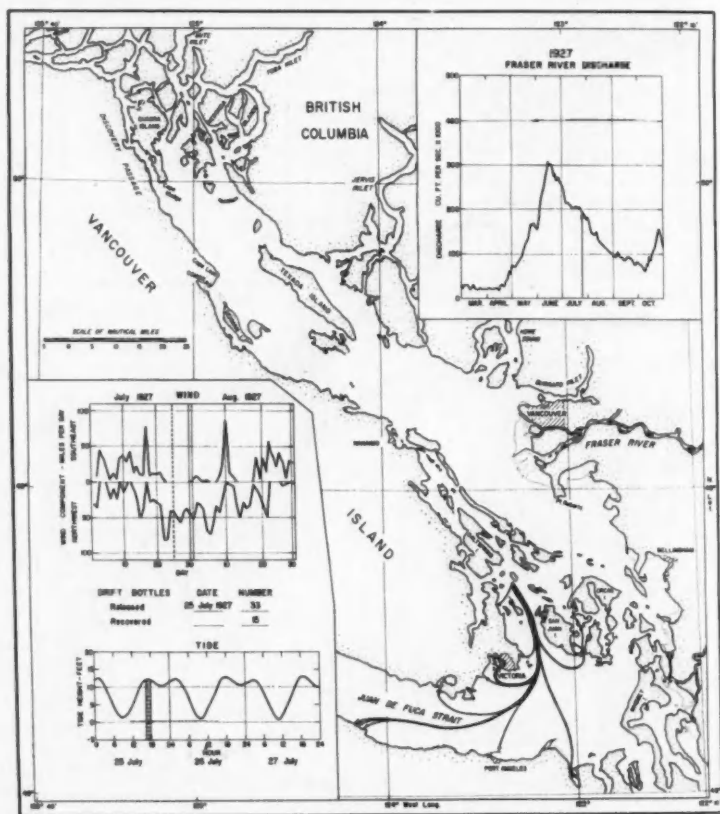


FIG. 7. Distribution of recoveries of drift bottles, Series 27.2, released on a line through Haro Strait, July 25, 1927.

Series 27.2 and 27.3 (Fig. 7 and 8) were released in Haro and Rosario Straits, respectively. Results of note in the recoveries from these series are that the drift of bottles in Haro Strait was southward into Juan de Fuca Strait while that in Rosario Strait was northward. These bottles probably responded to the southward bias of tidal currents in Haro Strait and northward bias in Rosario

Strait, normally present in these channels (Canadian Hydrographic Service, 1950, pp. 64-65).

During the period 20 July to 8 August, 1927, winds were almost continuously northwest. Drift bottles liberated at this time, series 27.4-27.8, represented in Fig. 9-13, all exhibited predominantly a southward drift. Figure 9, showing a release from Point Roberts to Sand Heads Lightship, indicates a strong drift from the Fraser River estuary toward Active and Boundary Passes. Recoveries in Boundary Bay from this series suggest a circulation in a large counterclockwise eddy in the southern part of the Strait of Georgia.

In a series liberated on a line from the Sand Heads Lightship to Bowen Island (Fig. 10), the characteristic movement of water from the northern part of the Fraser River estuary into Burrard Inlet is shown by the recoveries in outer Vancouver Harbour. This series also exhibited the drift across the Strait of Georgia to the passes among the Gulf Islands.

A series of drift bottles liberated 26 July on a line from Point Grey to Entrance Island (Fig. 11) showed considerably more scatter of recoveries along the perimeter of the Strait of Georgia than those of other series during July and August. However, only 3 bottles of the 48 recovered were taken from an area substantially north of the release line. A relatively large number of bottles was recovered from Burrard Inlet and Howe Sound and from Gabriola Island. Once again, there is evidence that bottles drifting into the southern part of the Strait of Georgia are shunted northward into Boundary Bay by the counterclockwise sweep of the currents in this part of the strait.

Drift bottle recoveries from a release made on a line from Active Pass to the Sand Heads Lightship demonstrated a dominant southward drift (Fig. 12). Three bottles did drift northward, two subsequently being recovered from outer Vancouver Harbour and the third from Thormanby Islands.

The final 1927 series was released on a line from Entrance Island to Point Grey (Fig. 13). With the exception of one return from Thormanby Islands, all recoveries were made from areas south of the release line. Four bottles were recovered from outer Vancouver Harbour. The large number of bottles taken in Boundary Bay had probably been swept northward from the San Juan Archipelago during a flooding tide.

1928 SERIES

Drift bottles were liberated in a number of releases during the latter part of May as well as in July and early August of 1928. A total of 466 bottles was released with a recovery of 213, a return of 45.7%. While drift bottles continued to be released in the southern part of the Strait of Georgia, some effort was extended during this year into local areas of the northern strait.

The first three 1928 series of drift bottles were released on 23 May. This was a period of rapidly increasing Fraser River discharge and of relatively large tidal ranges. Winds were moderately strong northwest on 23 May increasing during the following day.

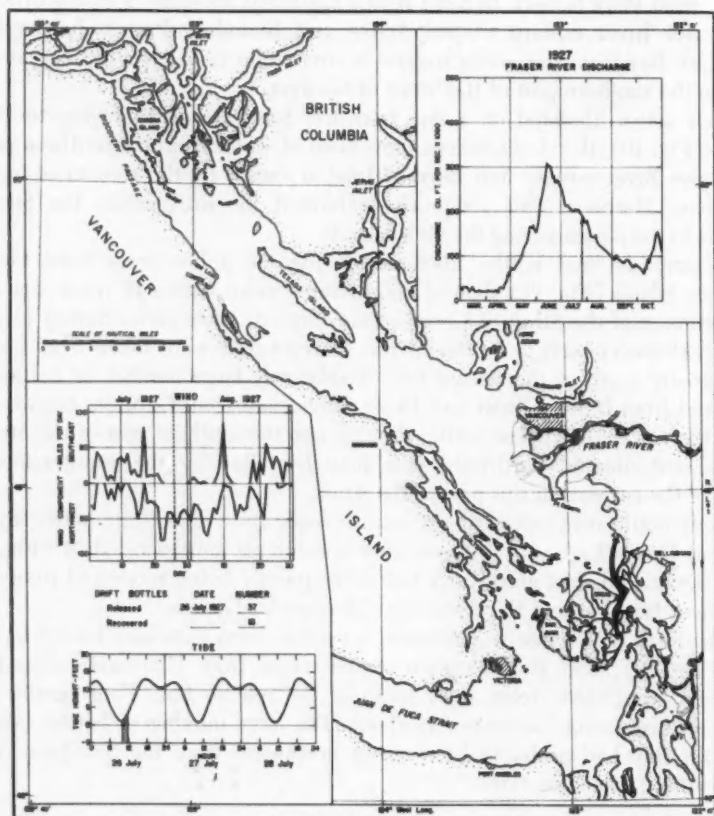


FIG. 8. Distribution of recoveries of drift bottles, Series 27.3, released on a line through Rosario Strait, July 26, 1927.

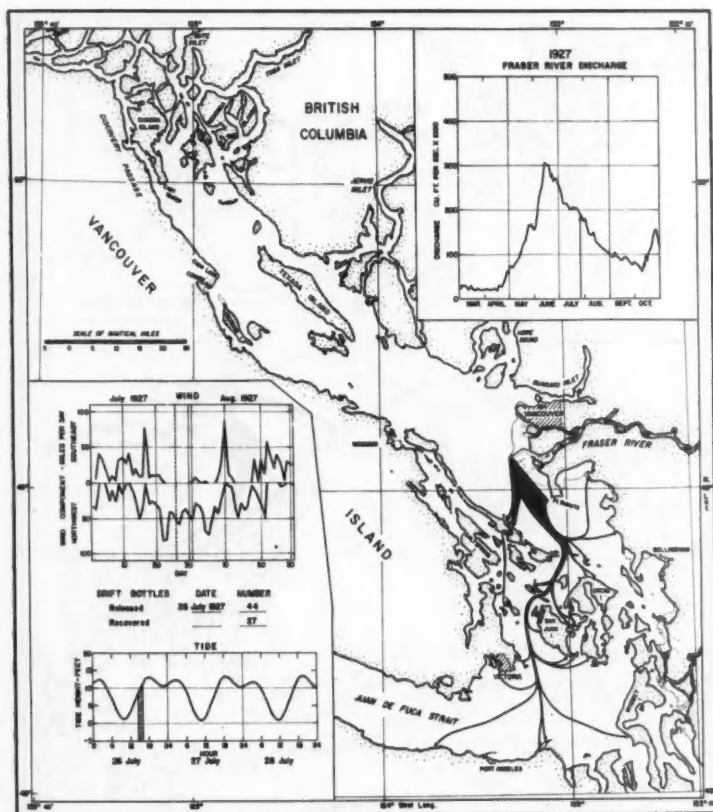


FIG. 9. Distribution of recoveries of drift bottles, Series 27.4, released on a line from Point Roberts Village to Sand Heads Lightship, July 26, 1927.

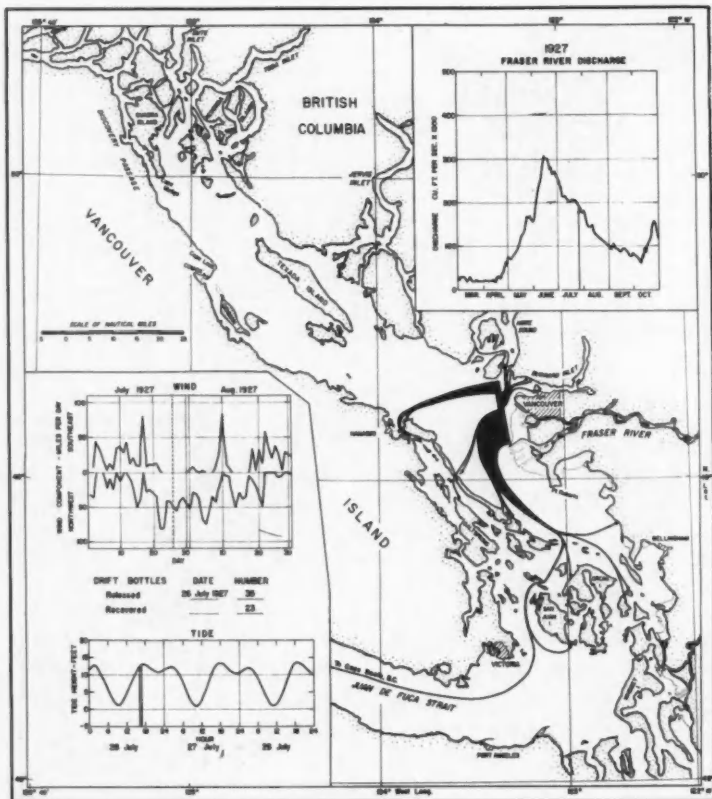


FIG. 10. Distribution of recoveries of drift bottles, Series 27.5, released on a line from the Sand Heads Lightship to Bowen Island, July 26, 1927.

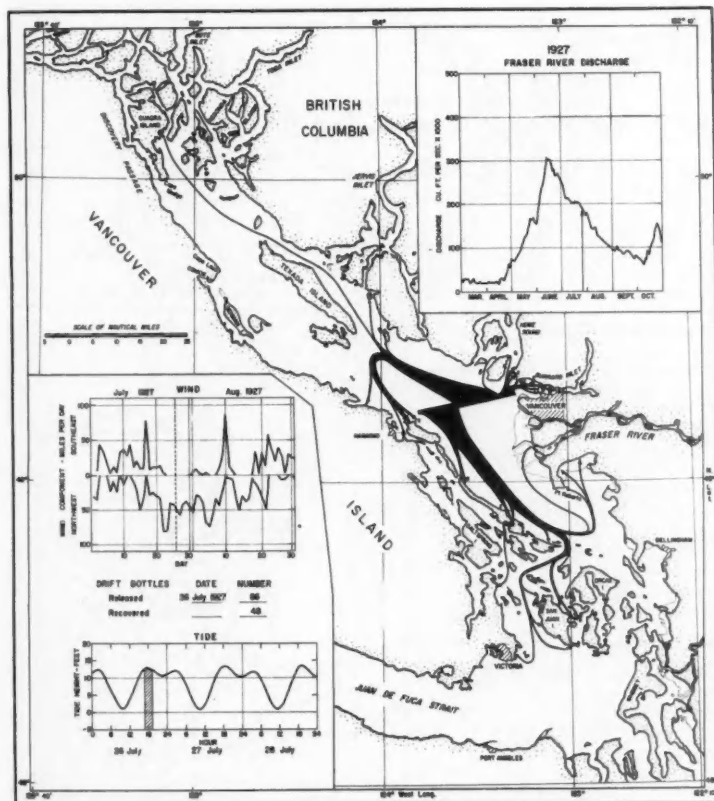


FIG. 11. Distribution of recoveries of drift bottles, Series 27.6, released on a line from Point Grey to Entrance Island, July 26, 1927.

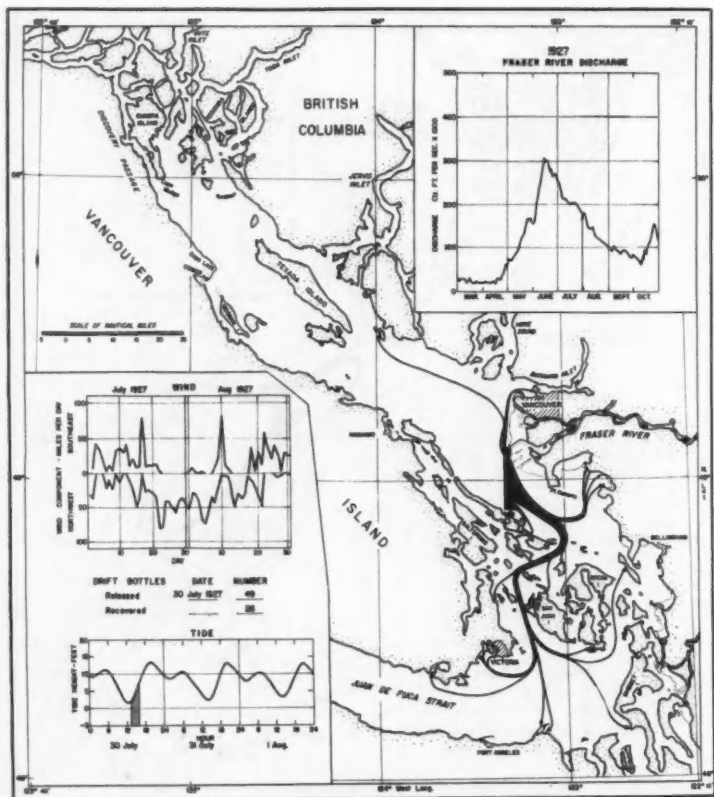


FIG. 12. Distribution of recoveries of drift bottles, Series 27.7, released on a line from Active Pass to Sand Heads Lightship, July 30, 1927.

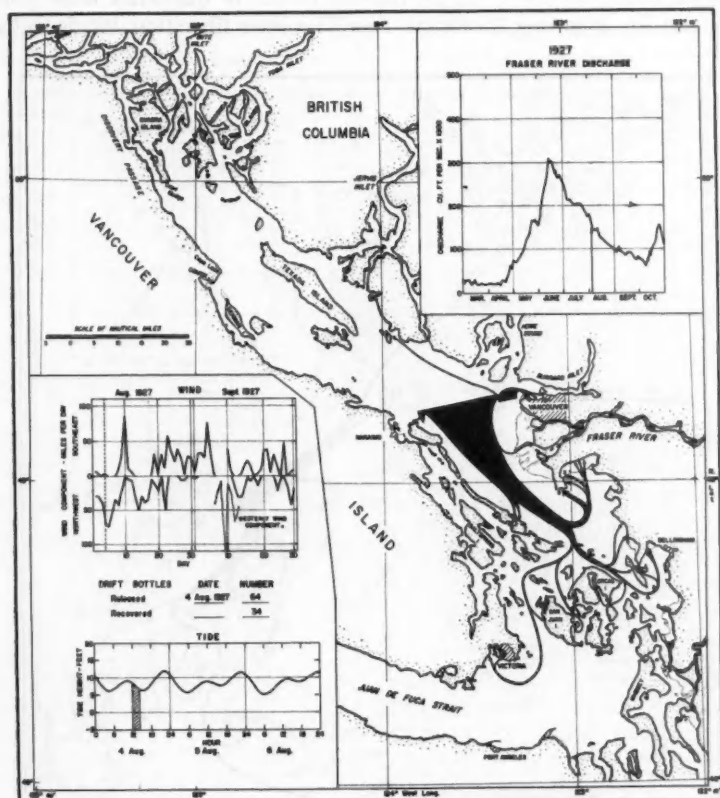


FIG. 13 Distribution of recoveries of drift bottles, Series 27.8, released on a line from Entrance Island to Point Grey, August 4, 1927.

In Fig. 14, where a series of drift bottles was released on a line from Porlier Pass to the Sand Heads Lightship, there was a recovery distribution suggesting that about half of the bottles drifted northward and half drifted southward of the release line. A drift from the Strait of Georgia into passes among the Gulf Islands was exhibited by the southward moving bottles. Winds were quite strong northwest on the day the bottles of this series were liberated and for one day following liberation. Two days after liberation, winds shifted to

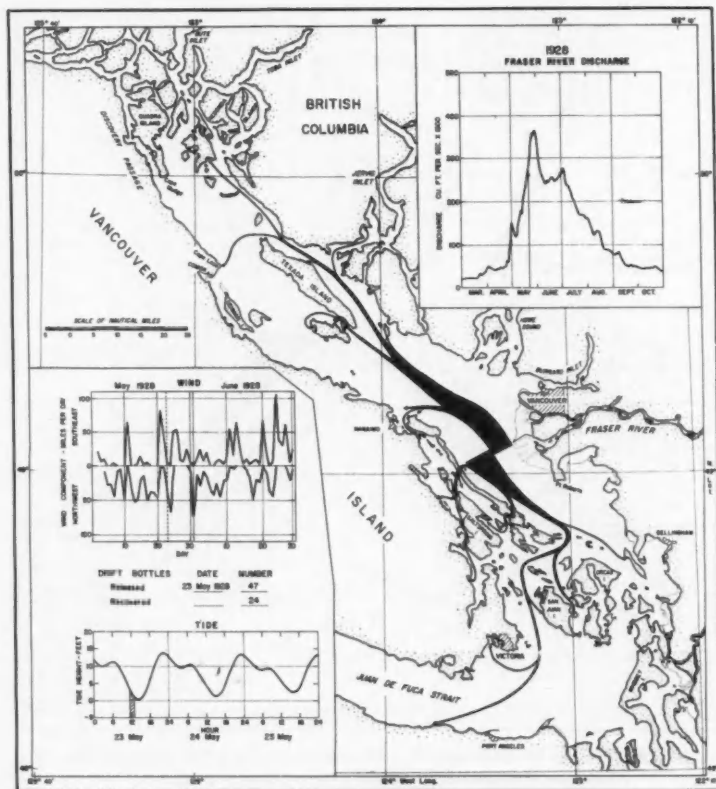


FIG. 14. Distribution of recoveries of drift bottles, Series 28.1, released on a line from Porlier Pass to Sand Heads Lightship, May 23, 1928.

fairly strong southeast. All bottles probably commenced drifting southward or into the passes among the Gulf Islands immediately following liberation. As the wind changed to southeast, the bottles which were still in the open strait probably commenced a northward movement.

A series released along the southern part of the Fraser River estuary, shown in Fig. 15, resulted in widespread distributions all around the Strait of Georgia. The majority of the bottles drifted into the Gulf Islands and the southeastern coast of Vancouver Island. Others drifted into Boundary Bay, Howe Sound and the northern part of the strait. A combination of driving forces was probably

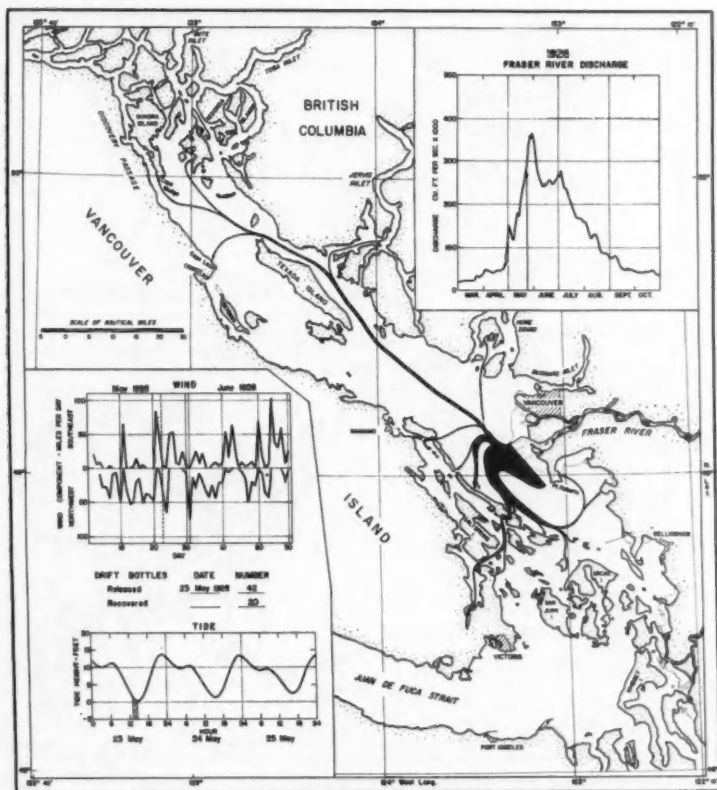


FIG. 15. Distribution of recoveries of drift bottles, Series 28.2, released on a line from the Sand Heads Lightship to Point Roberts, May 23, 1928.

responsible for these scattered recoveries. The northwest wind and the runoff from the Fraser River moved the drift bottles toward the Gulf Islands soon after liberation. The southeast wind, which came two days later, then carried some of the bottles northward.

The predominant drift of bottles in a series released on a line from Point Roberts to Active Pass (Fig. 16) was into the Gulf Islands, with 12 out of the 14 bottles recovered landing on Galiano Island. Because most of the bottles were recovered only a day or two following release, it is presumed that the large tides, high Fraser River discharge and northwest wind during and following the release were responsible for the resultant drift of the bottles.

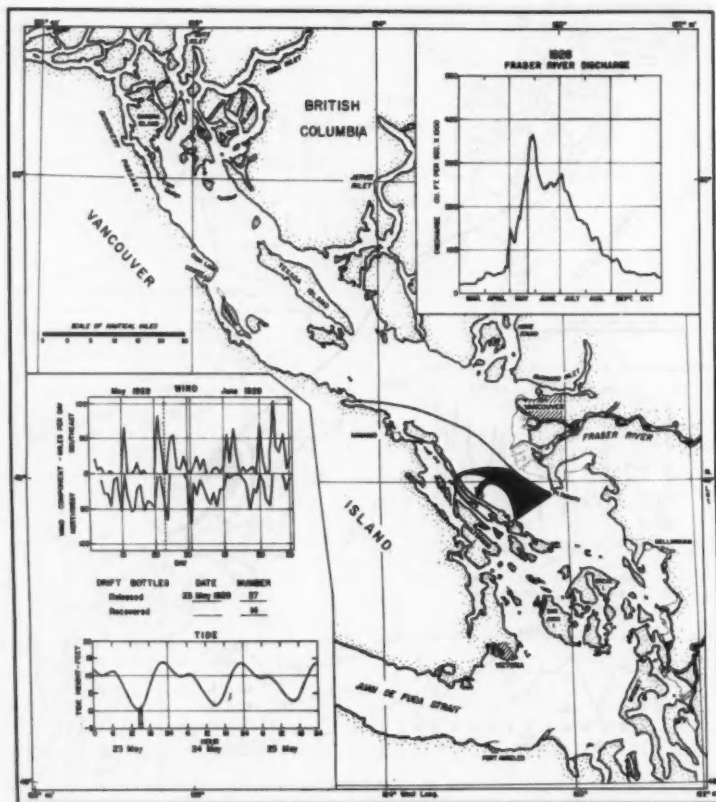


FIG. 16. Distribution of recoveries of drift bottles, Series 28.3, released on a line from Point Roberts to Active Pass, May 23, 1928.

One series of drift bottles was liberated 6 July on a line from Burrard Inlet to Departure Bay (Fig. 17). The exact time of liberation is unknown since original records do not give this information, but it is presumed that the release was made between 1800 and 2100 during the latter half of a large flood tide.

Out of the 37 bottles released, about half were recovered. Half of the returns came from points on the mainland and adjoining islands just north of the line of liberation. The other half came from points to the south. During the week following liberation, winds were variable from day to day. Most of the bottles

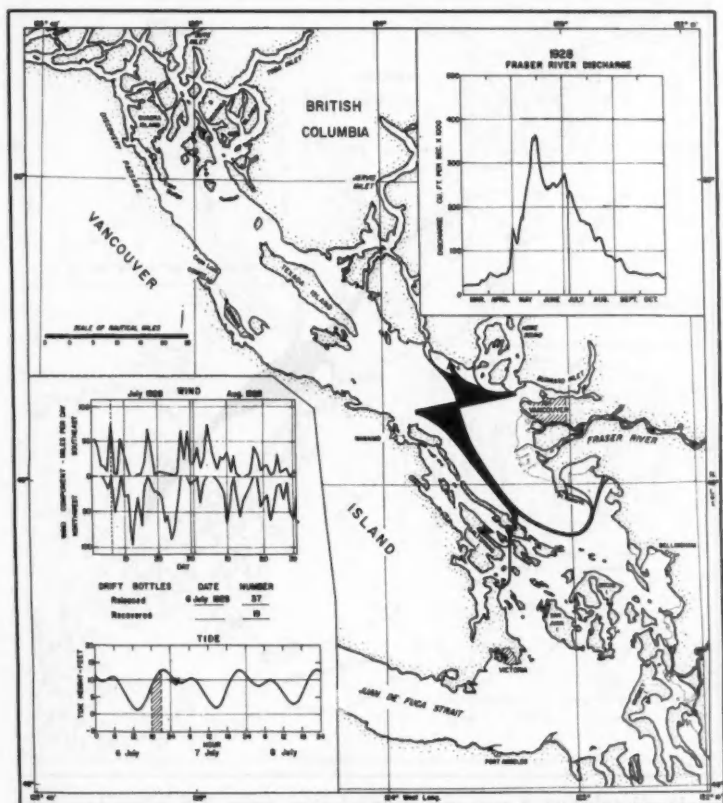


FIG. 17. Distribution of recoveries of drift bottles, Series 28.4, released on a line from Point Grey to Entrance Island, July 6, 1928.

recovered in the Howe Sound area and to the north were presumably washed ashore by southeast winds some time around 10 July, since many of the returns from that area were so dated. Bottles in the southern area were recovered much later and were probably carried southward by northwest winds, which commenced a day following release and continued for several days.

A number of point releases with bottles liberated at given time intervals were made during the period 25-27 July, among the Gulf Islands. In general, recoveries from such releases were made along shores among the islands not too far away from the origin.

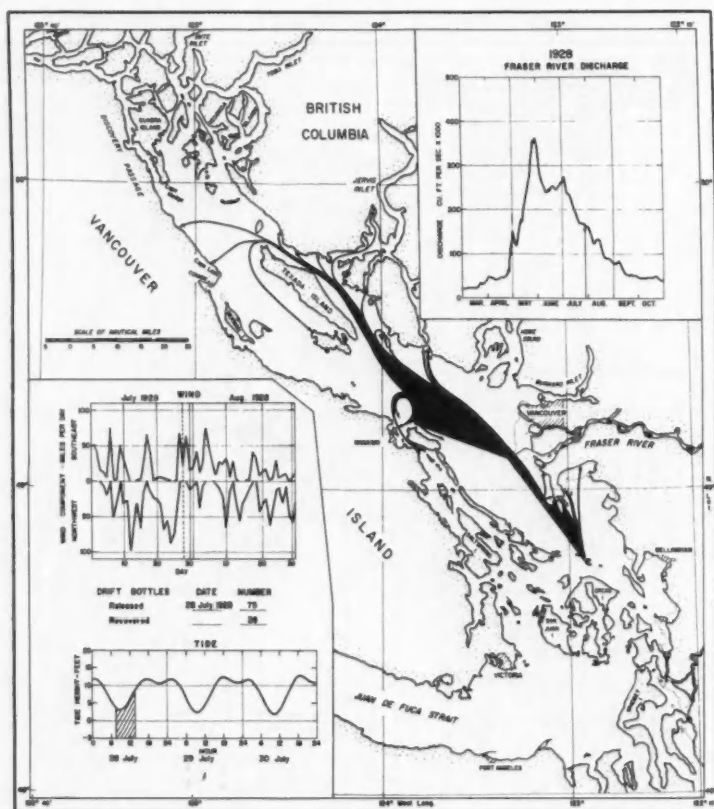


FIG. 18. Distribution of recoveries of drift bottles, Series 28.8, released on a line from Sucia Island to Sand Heads Lightship and then to Entrance Island, July 28, 1928.

On 28 July, during southeast winds and a rising tide, a series of 75 drift bottles was released, 1 bottle every 5 minutes while travelling at 8 knots, on a line from Sucia Island to Sand Heads Lightship and thence to Newcastle Island (Fig. 18). Bottles from the southern section of this release line drifted in fairly large numbers onto the shores around Point Roberts. Recoveries from the northern section of the line were scattered along the northeastern part of the Strait of Georgia with some landings in the vicinity of Gabriola Island, Lasqueti Island,

and Cape Lazo. The predominantly northwestward drift was probably due to southeast winds of moderate strength, which prevailed during the period of release and for about 12 days following release. Two of the bottles from this series were recovered from Jervis Inlet, showing possibilities of up-inlet drift.

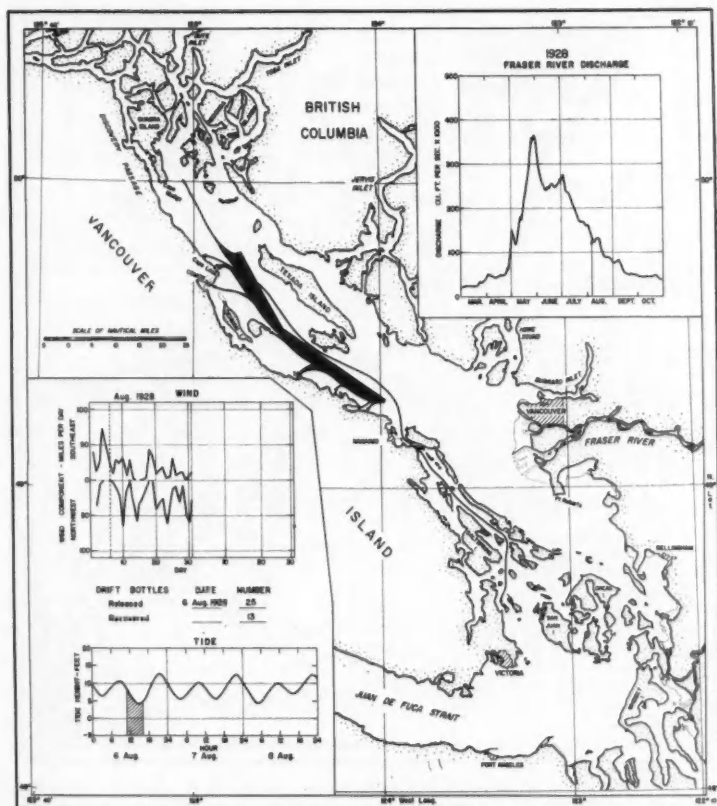


FIG. 19. Distribution of recoveries of drift bottles, Series 28.9, released on a line from Winchelsea Island to the north end of Texada Island, August 6, 1928.

A release of bottles was made on 6 August from approximately Winchelsea Island to the north end of Texada Island (Fig. 19). Most of these bottles drifted to the adjacent shore on Vancouver Island. Winds were lightly southeast at time of release followed in 3 days by strong northwest winds.

Drift of surface currents at the extreme northern end of the Strait of Georgia was tested by liberation of bottles on a line from Hernando Island to Quathiaski

Cove (Fig. 20). Of the 19 bottles liberated, 3 were recovered from points south of the line of release and 5 drifted northward into channels among the northern islands.

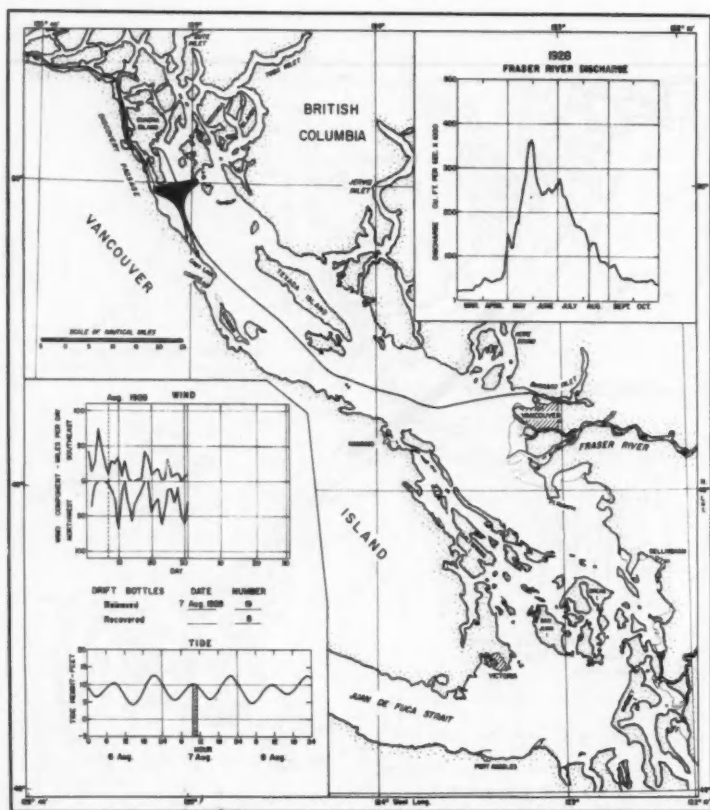


FIG. 20. Distribution of recoveries of drift bottles, Series 28.10, released on a line from Tongue Point, Hernando Island, to Quathiaski Cove, Quadra Island, August 7, 1928.

1929 SERIES

Drift bottle releases in 1929 were confined mainly to small groups of bottles at various points within the Strait of Georgia. Out of a total of 242 bottles released, 111 were recovered, a return of 45.9%. All releases in 1929 were carried out on four days, 9-10 August and 16-17 August. Winds from day to day were variable following the releases, with northwest winds 9-10 August, southeast winds 11-13

August, southwest 14 August, variable east and west 15 August, strongly north-west 16 August, shifting to strong east-southeast for the following week.

Only a number of selected charts are shown for the 1929 releases and distribution of recoveries. Drift bottles released in groups along the Gulf Islands and

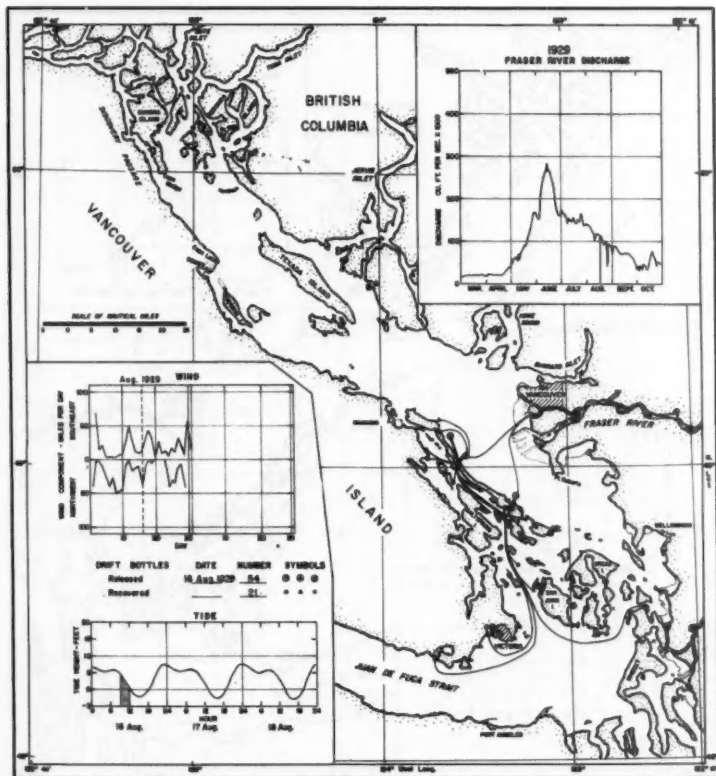


FIG. 21. Distribution of recoveries of drift bottles, Series 29.3a, released from points along the Gulf Islands, August 16, 1929.

in Boundary Pass on 16 August are represented in Fig. 21 and 22. The predominant movement of bottles was apparently southwestward in both series judging from the number of recoveries along the shores of the Gulf Islands. A small number of bottles was recovered from eastern Juan de Fuca Strait. Two bottles were recovered at some distance up the middle arm of the Fraser River. Because of the delay in recovery of these bottles after release, the possibility of accidental dragging by scow or log boom up the river is suspected.

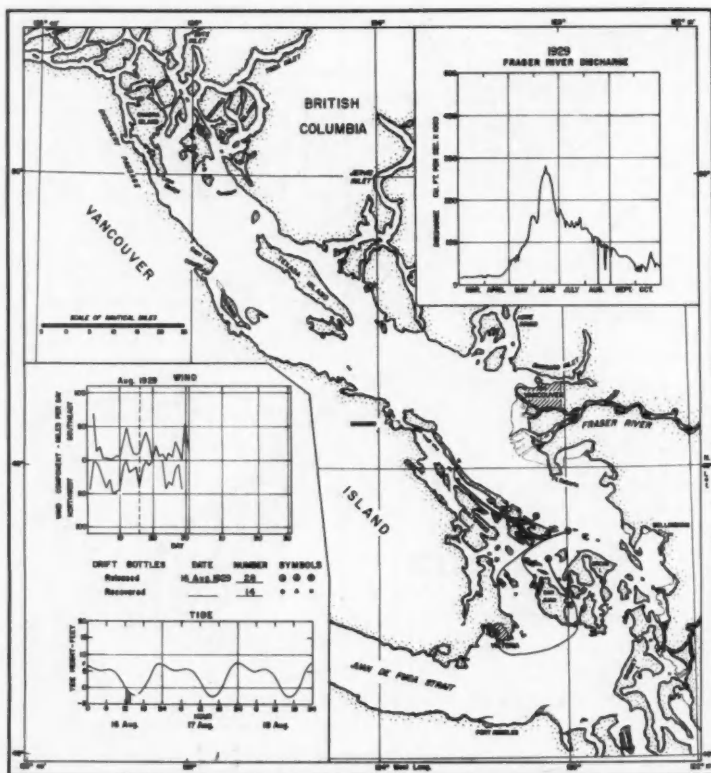


FIG. 22. Distribution of recoveries of drift bottles, Series 29.3b, released from points in Boundary Pass and vicinity, August 16, 1929.

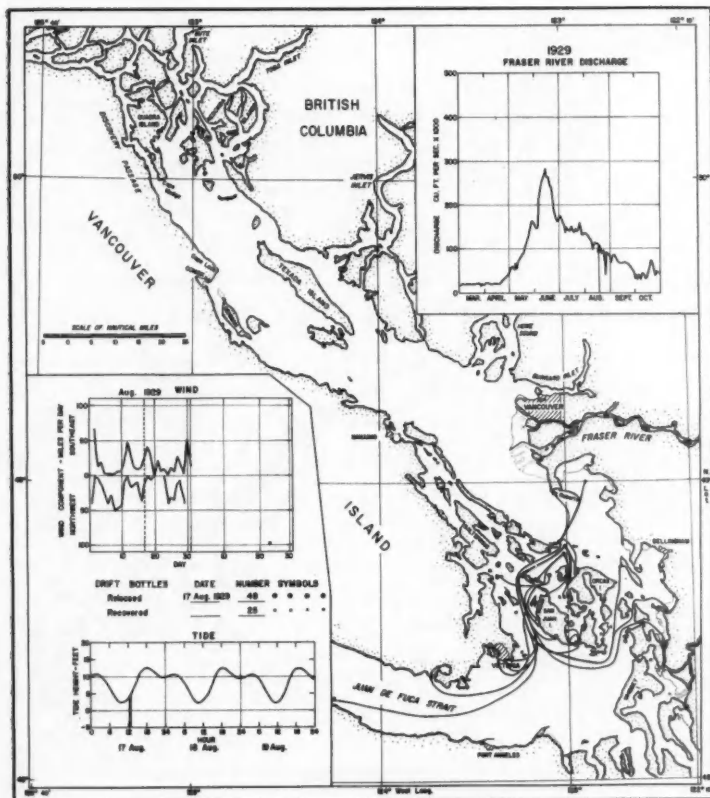


FIG. 23. Distribution of recoveries of drift bottles, Series 29.4, released from points in Boundary Pass, August 17, 1929.

Releases of groups of bottles were made at various points in Boundary Pass on 17 August (Fig. 23). With the exception of three bottles from a release point near Tumbo Island, which landed at Point Roberts and in Boundary Bay, drift

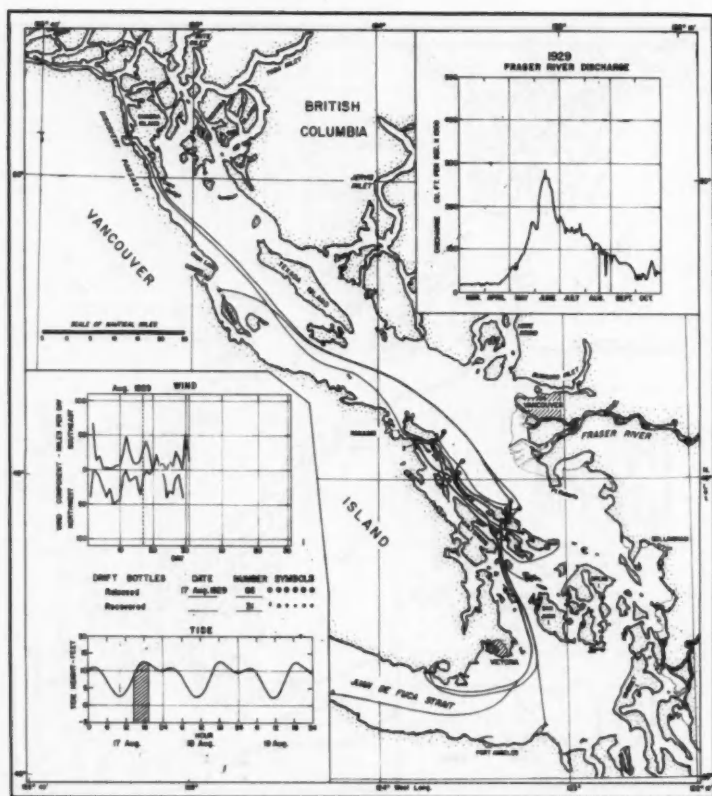


FIG. 24. Distribution of recoveries of drift bottles, Series 29.5, released from points along the Gulf Islands, August 17, 1929.

of the bottles was southward. Release points of a series of bottles liberated along the Gulf Islands also on 17 August are shown in Fig. 24. To a large extent, these bottles drifted onto the shores of the Gulf Islands and several were recovered at points along Juan de Fuca Strait. Three isolated bottles from three different groups were recovered from points in the northern Strait of Georgia and Johnstone Strait.

1931 EXPERIMENT ON THE EFFECT OF DRAGS ON DRIFT OF BOTTLES

In all, 26 pairs of bottles were released, out of which 10 bottles with drags and 8 without drags were recovered (Fig. 25). One pair of bottles apparently moved together, since both the bottle with drag and that without were recovered

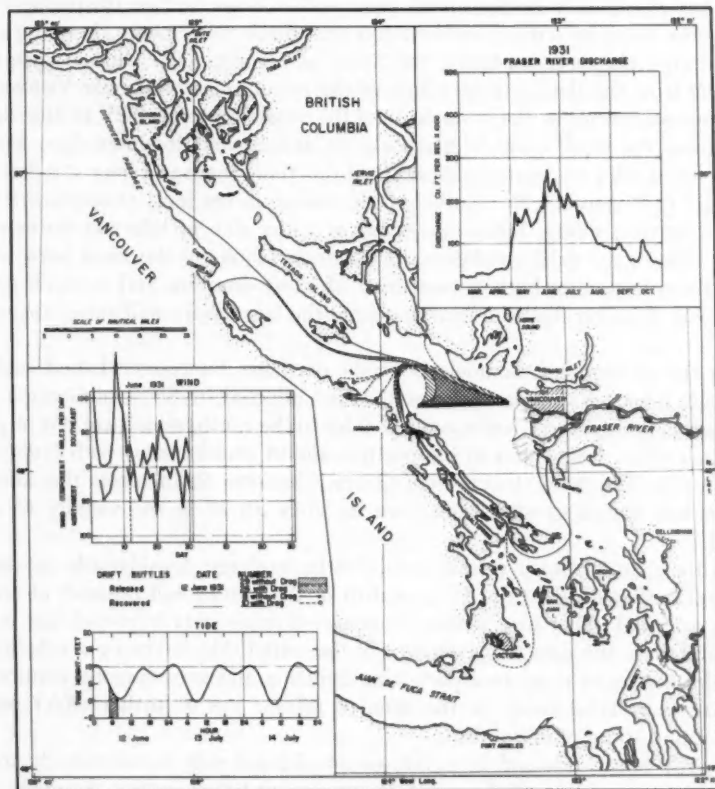


FIG. 25. Distribution of recoveries of drift bottles, with and without drags, released on a line from Point Grey to Entrance Island, June 12, 1931.

from approximately the same locality. Returns from one pair came from an area north of the line of liberation, but the bottles were recovered from opposite sides of the Strait of Georgia. One pair of bottles separated and landed at points north and south of the line of liberation. In general, the distribution of recoveries was scattered without a marked movement in any particular direction. A large proportion of both types of bottles drifted onto the shores of Vancouver Island between Gabriola Island and Northwest Bay.

FACTORS INFLUENCING DRIFT OF BOTTLES

In the Strait of Georgia there are three major factors responsible for surface currents and drift bottle propulsion—tide, wind and runoff.

TIDE

Characteristically of the mixed type with a large diurnal inequality in the low waters, tides are a major influence on drift bottle movements along the shores and through channels bordering the Strait of Georgia. The diurnal inequality, resulting from the declinational effect of the moon, is greatest near Victoria and decreases northward as the main body of the strait is approached. In the vicinity of Victoria, the small daily tides are almost non-existent for more than half the month when tides are virtually diurnal. At this time, there is a long stand at high tide for 7 to 10 hours, with relatively little change in sea level (Canadian Hydrographic Service, 1950). Little movement of water due to tide can be expected during these static tidal conditions. In channels adjoining the main body of the strait, there is usually both a movement of short duration and a much swifter movement of longer duration resulting from the large and small tidal ranges in a cycle.

In the network of channels between northern Vancouver Island and the mainland, tides are complex because they are affected by Strait of Georgia tides to the south and Queen Charlotte Strait tides to the north, which are out of phase with each other. Low water to the north is almost simultaneous with high water to the south. The flood stream from Queen Charlotte Strait meets the southern flood, which has progressed from Juan de Fuca Strait, in the vicinity of Cape Mudge.

In their drift from a release area, bottles undergo considerable movement back and forth with the tide. The net drift of the bottles will depend, of course, on the net tidal effect in addition to other influences which propel the bottles forward. Often, the directing influence of the initial tide following a release will cause the bottles to move in a particular direction and subsequently continue in that direction. Tidal range at the time of release has a further effect on the direction and speed of initial drift.

A drift bottle released in a tide-swept channel will move initially in the direction of the existing tidal current. Its movement following the change in tidal current direction will depend on the current in the area into which it has moved. Thus, a bottle released in Active Pass will drift with the tidal current prevailing in the pass at the time of release. Because the pass is relatively short and the current is swift, the bottle will undoubtedly move either into the Strait of Georgia or into Trincomali Channel on one stage of the tide. The chances are that the bottle will not return to Active Pass on a subsequent stage of the tide, but instead will move with the currents in the Strait of Georgia or Trincomali Channel.

In a long channel, such as Discovery Passage or in a long inlet, where a drift bottle is unable to move out completely in the course of one tidal stage, the bottle may oscillate back and forth with the tide for some time. Its net movement in a given period will depend on other forces, which drive the bottle in one direction.

The asymmetry of the current, where there is a greater flow in one direction than in another, is the usual cause for a net displacement of a drift bottle in such areas.

No marked tidal movement occurs in the main basin of the Strait of Georgia (unpublished data on anchor station observations). Tides are manifested in a mere rise and fall of water level. Here drift bottle movements are dependent on other external forces.

WIND

Surface currents in inshore regions are sometimes largely wind-driven (Waldichuk and Tully, 1953). Thermal and salinity stratification allows wind stress to generate considerable horizontal movement in the light surface layers of water. This is particularly true in the Strait of Georgia, where a large volume of runoff creates a brackish upper layer and winds can be of considerable strength.

Winds in the Strait of Georgia are, to a large extent, directed along a northwest-southeast direction, i.e., along approximately the axis of the strait. A slight deviation from the northwest-southeast wind circulation occurs in the southern Strait of Georgia. In this area, surface winds have a predominant northward movement along the coast of British Columbia and Washington near the international border (Waldichuk, 1957, p. 417). There is a prevailing easterly wind in Vancouver and vicinity throughout the year, although the frequency of westerly and northwesterly winds increases during the summer months. Along the southeast coast of Vancouver Island, including the Gulf Islands, southeast winds prevail during the spring and summer months of the year. This wind direction shifts to southwest along Juan de Fuca Strait in the vicinity of Victoria.

The effect of wind is greatest in the open waters of the Strait of Georgia. Among the islands at the approaches to the strait in the south and in the north, the shelter of land masses reduces the effect that wind might otherwise have on drift of surface water. In these areas also, the tidal effect is so much greater than the other forces that winds become only a minor consideration.

In the charts showing drift bottle distributions, only the northwestern and southeastern components of winds have been represented. While these are probably the most important wind directions, there were also winds from other directions, which were significant for short periods. Winds at Vancouver are not entirely representative of those in the whole Strait of Georgia. However, deviations are probably only large enough in the southern strait to make much difference in interpretation of effect on drift bottle movement.

Winds have other effects than merely moving surface water northwesterly or southeasterly in the Strait of Georgia. Strong onshore winds in some local areas resulted in considerable numbers of bottles being beached.

RUNOFF

Movement of fresh water from the Fraser River into the Strait of Georgia creates a surface layer of brackish water, which undergoes a continuous seaward displacement. The magnitude of the Fraser River discharge at the time of drift bottle liberation can be expected to have an effect on the direction and rate of

movement of drift bottles. Effect of runoff is particularly noticeable in drift bottle movements during or near the peak discharge of the Fraser River.

It is of some interest to note that the Fraser River discharge curves shown in all the charts of releases and recoveries of drift bottles vary considerably in shape from year to year during the period 1926-1929. A typical hydrograph for the summer discharge is similar to those shown for 1927 and 1929 with one large peak between mid-June and early July. During other years, when temperatures and the melt of snow in the drainage basin of the Fraser River deviate from trends in average years, two smaller peaks in discharge may occur, as shown in the hydrograph for 1926. Accordingly, the effect of summer runoff can be expected to vary from year to year. The flow of water from the Fraser River estuary during a large peak discharge is many times greater than that during periods of small flow. Consequently, the drift of bottles driven by the fresh water will be greater and more widespread during periods of freshet than during periods of small runoff.

DISCUSSION

The success of a drift bottle experiment depends on the support of the public. Recoveries of drift bottles are almost entirely dependent on human habitation along shores on which the bottles land. Where beaches are frequented by large numbers of persons, the recoveries of bottles landing there will be high. On the other hand, rocky and wooded shores are often less attractive to visitors and, as a result, would yield only a small number of returns. Moreover, bottles landing on rocky shores are subjected to harsh treatment by the action of waves and surf with the possibility of breakage. Consequently, the proportions of drift bottle card returns from the same number of bottles landing on a popular beach and on an unattractive, rocky shore are likely to be very different. This can lead to an unreal drift pattern distorted by the unevenness in shore population. All the drift bottle experiments described herein were carried out during spring and summer, when sea shores were probably most fully populated by summer campers and other seasonal visitors, and adjacent waters were plied by numerous pleasure craft.

Unless a drift device is actually followed, it can only provide information derived from time and place of release and time and place of recovery. The net distance moved in the time between release and recovery and the net direction can be estimated. It is presumed that there is considerable meander with the tide and wind before the bottles are ultimately beached or picked up by some boat at sea. Because drift bottles are not necessarily recovered immediately after they land on shore, the speed of drift calculated is always a conservative value.

Certain features associated with man's settlement along the Strait of Georgia have contributed to some of the characteristics in the recovery patterns. Large numbers of recoveries in the vicinity of Vancouver and Victoria can be partly attributed to the large populations in these centres. Drift bottles were often reported to be caught in fish traps at Sooke, Point Roberts and on islands adjacent

to the Washington coast north of Puget Sound. While there were not very many open-water recoveries, most of these occurred in waters heavily fished by commercial and sports fishermen.

Where there were large populations in areas of frequent onshore winds and surface currents, recoveries were always high. Movement of Fraser River water into Burrard Inlet on certain stages of the tide was responsible for the relatively large number of bottles recovered from outer Vancouver Harbour. A movement of drift bottles toward shore in the area northwest of Howe Sound resulted in large numbers of recoveries in the vicinity of Roberts Creek (Fig. 6). This landward drift was probably caused by strong onshore winds immediately following release of bottles nearby.

Certain experimental errors entering into drift bottle experiments can be summarized as follows:

(a) Bottles used in some experiments were ballasted so near the critical point between sinking and floating that they floated in sea water and sank in fresh water. Only one series of bottles, No. 251-265 (Table I), was reported in the field notes to be observed sinking in Fraser River water. The consequence of such an occurrence is only that recoveries will be small.

(b) The possibility of accidental dragging of drift bottles by boats and log rafts cannot be overlooked. Only one such incident was reported in a returned card.

(c) Often local names have been used on card returns to describe locations of recoveries. Some of these names do not appear in the *Gazetteer* (Canadian Board on Geographical Names, 1953) nor in the *British Columbia Pilot* (Canadian Hydrographic Service, 1944) and may have been changed in the course of the 30 years from the time the data were collected to the time they were analyzed. In most of these cases, it is considered that a fairly reasonable interpretation has been made in pin-pointing the recovery location from postal marks and address of the finder.

Notwithstanding these possible errors in the results of the drift bottle experiments, the percentage recoveries were usually large enough to give a fairly reliable representation of bottle movement.

A comprehensive discussion of results from all series of drift bottle releases will not be attempted here. However, there are a number of generalizations which can be made from an over-all analysis:

1. Bottles released anywhere along the Fraser River estuary north of the Sand Heads Lightship usually landed in some numbers in Burrard Inlet, along English Bay and on the north shore of the inlet west of the First Narrows. Some of the bottles of such series drifted even farther northward and were recovered from the shores of Howe Sound. Such a drift has been substantiated in more recent free float experiments (Canadian Hydrographic Service, 1952; Vancouver and Districts Joint Sewerage and Drainage Board, 1953) and in analyses of movements of silty Fraser River water from aerial photographs (Fjarlie, 1950).

2. A release of bottles on a line from Point Grey to Entrance Island resulted in a drift northward or southward depending on wind, tide, and runoff at the time

of release. Under calm conditions, bottles on the east end of the line drifted northward with the prevailing water flow on that side of the Strait of Georgia. Bottles on the west end of the line usually drifted southward following the dominant southward flow of water along the Vancouver Island side of the strait.

3. When bottles drifted into the southern part of the Strait of Georgia, there were almost invariably some recoveries in Boundary Bay. This is probably the result of a counterclockwise circulation in the southern part of the Strait of Georgia as well as a strong onshore surface current into Boundary Bay from Rosario Strait.

4. Of the bottles drifting into Juan de Fuca Strait, many were recovered at the southern end of Vancouver Island. The high population density was partially responsible for the high recoveries on this part of the coast. However, it is also possible that tidal currents circulate in an eddy pattern in this region or that there is a strong sweep of currents against the peninsula on which Victoria is located.

5. A large percentage of drift bottles which reached the north end of the Strait of Georgia drifted into channels separating the northern part of Vancouver Island from the mainland. This is an indication that there is a net northward drift of surface water through Discovery Passage and adjacent channels.

6. Among bottles released along the Fraser River estuary, usually a large proportion drifted toward the passes among the Gulf Islands, particularly toward Active Pass. From the short time after release that these bottles were recovered, it can be presumed that they drifted there on one large ebb tide.

7. Regardless of wind, bottles released in Haro Strait and other channels on the west side of the San Juan Archipelago drifted southward. Those released in the eastern channels (Rosario Strait) drifted northward, in accordance with net flow of surface water in these channels (Canadian Hydrographic Service, 1950, pp. 64-65).

8. It is of interest to note that, while some dominance was shown for a southward drift through Haro Strait, a considerable number of bottles drifted through San Juan Channel and other small passages in the San Juan Archipelago. The unusually large number of bottles recovered from these islands was partially attributable to the large number of summer dwellers along their shores.

9. The predominant flow of water through the passages among the Gulf Islands occurs in a southwesterly direction from the Strait of Georgia into the inner channels between the Gulf Islands and Vancouver Island.

10. Drift speeds calculated from the earliest drift bottle recoveries following a release are of the order of 26 cm./sec. (0.5 knot) for the drift from the Fraser River estuary to Active Pass. Drift speed calculated for drift bottles released near Point Grey and recovered near Roberts Creek exceeded this considerably. The average speed for drift of bottles through the Strait of Georgia was about 5 nautical miles per day or 10 cm./sec. (0.2 knot).

While the drift of bottles up inlets and into river mouths was not common, there were the occasional bottles which drifted against the dominant seaward flow of surface water. This movement was probably caused by a favourable combination of wind and tide, which carried the bottles in the upstream direction. The occasional movement of surface water up inlets has probably been the cause

of the natural spread of larvae of the Pacific oyster, *Crassostrea gigas* (formerly *Ostrea gigas*), introduced into Ladysmith Harbour during 1925 (Elsey, 1932). The oyster larvae settled in suitable locations among the Gulf Islands (Elsey and Quayle, 1937) during early years of spawning, and subsequently drifted into Jarvis Inlet, Pendrell Sound, and other areas bordering the northern part of the Strait of Georgia (Quayle, 1955). While the drift of surface water from among the Gulf Islands into inlets at the northeastern end of the Strait of Georgia is one of the more unlikely directions of movement of water through the strait, evidence from the recoveries of some bottles which drifted into these inlets points to definite possibilities of such movements.

Judging from the fairly regular movement of bottles into Boundary Bay, it can be inferred that there is a movement of Fraser River water in a counterclockwise circulation along the shores of Boundary Bay. That there is a certain factual basis for the early belief of scientists and fishermen that salmon moved along the shores of Boundary Bay and edged close to Point Roberts in their migration to the Fraser River seems to be borne out in these drift bottle findings. Salmon possibly detect Fraser River water in Juan de Fuca Strait or at least in Rosario Strait and in other channels leading to the southern Strait of Georgia. Depending on the tide, they may move directly toward the Fraser River estuary or they may migrate into Boundary Bay, according to where the greatest concentration of fresh water occurs. Some of the fish may be "navigating" by following the shoreline.

While the experimental results were inconclusive in establishing any marked variation in the direction or rate of drift of bottles with drags and those without, they did show that there is a certain scatter in drift of both types of bottles.

SUMMARY

1. A total of 1,636 drift bottles was released in the Strait of Georgia during the years 1926-1929 inclusive. From these, 672 cards were returned, a recovery of 41%.
2. An experiment designed to show any possible difference between the drift of bottles with drags and those without drags gave inconclusive results.
3. Recovery of drift bottles shows that (a) wind is a major driving force in the open Strait of Georgia; (b) tidal currents are dominant in channels bordering the strait; and (c) runoff effects are particularly strong along the Fraser River estuary.
4. Major features in the circulation of surface water, as inferred from drift bottle results, are (a) large counterclockwise circulation in the whole body of the Strait of Georgia; (b) a smaller counterclockwise gyral in the southern strait; (c) a net seaward flow at the northern and southern approaches to the strait; and (d) a fairly consistent across-channel flow from the Fraser River estuary to passes among the Gulf Islands.
5. Current speeds calculated from drift bottle results are an average maximum of 26 cm./sec. (0.5 knot), when the bottles were driven strongly in one direction by tidal currents, runoff, and wind. On the average, current speeds are 10 cm./sec. (0.2 knot).

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Dr. N. M. Carter and Mr. J. P. Tully carried out the 1931 experiment to determine the effect of drags on drift bottle movements, and their contribution is duly acknowledged.

Thanks must also be expressed to those many people frequenting the sea shore and on boats, who retrieved bottles and returned cards giving the necessary information.

Fraser River discharge data have been plotted from published records of the Dominion Water Power and Reclamation Service (1927-1937) of the Department of the Interior, Canada. Wind data for Vancouver City have been kindly furnished by the Meteorological Division of the Department of Transport. Finally, I should like to thank Drs. W. A. Clemens and N. M. Carter for reading the manuscript and making valuable suggestions.

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Review of Certain Environmental Factors Affecting the Production of Pink and Chum Salmon¹

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ABSTRACT

The relation between stock and numbers of spawners is obscured by annual environmental changes. Stream discharge at the time the spawners are migrating upstream, at the time when the eggs are in the early stage of incubation, and extreme discharge during the period eggs and alevins are in the gravel can impose an 8-fold variation in the stock resulting from a given number of spawners in one area. Ocean conditions soon after the fry enter the sea have been observed to increase or decrease survival by a factor of 3. The density of spawners that produces the greatest numbers of fry is related to the average permeability of the stream bottom. Preliminary data indicate that more spawners could be used to advantage in most areas of the coast.

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INTRODUCTION

THE STOCKS OF PINK AND CHUM SALMON (*Oncorhynchus gorbuscha* and *O. keta*) in British Columbia waters have exhibited marked fluctuations over the years. No really comprehensive analysis of the relation of these to environmental factors has yet been made, to establish correlations and see what causes have been followed by what results. One reason that this has not been done is that there are many stocks and many environments, so that the physical task of assembling all the data that might be pertinent is a formidable one. Another obstacle is that,

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while quite a number of series of temperature and rainfall records exist at various points, their relation to conditions in specific spawning streams is often conjectural, or at least would require detailed knowledge of local geography. For example, a hot, clear summer may dry up many small coastal streams, but maintain a good flow in those fed by snow and ice melting at high elevations. An additional difficulty is that catch statistics for pink and chum salmon have only since 1951 been available on a satisfactory local basis, and even to-day many fisheries take mixtures of populations so that it is possible to locate the streams of their origin only within a broad stretch of coastline. Still another trouble is that, in general, environmental and biological conditions tend to be most favourable near the *middle* of their range of variation. Too much water is as bad as too little, too many eggs may produce no more fry than too few. Thus we should, *a priori*, expect *curved* rather than linear correlations between spawning conditions and resulting stocks, and these of course are much harder to demonstrate than straight-line relationships.

On the other hand, there have been quite a number of instances where extremes of natural conditions have been followed by sharp declines in the size of the stock of pink or chum salmon in a large river, or along a broad section of the coast. Usually a causal relationship is a reasonably strong presumption. In addition, there are a few regions of the province where data on temperature, rainfall or stream discharge can be related to salmon production over a fair number of years, and where these factors have varied over a wide enough range to give very suggestive relationships.

Finally, the detailed spawning-stream studies of the Fisheries Research Board at a number of sites have provided definite information on their fry production under a variety of conditions, and similar conditions have also been examined in the laboratory.

Without claiming complete objectivity or randomness in the search for examples, it seems useful at this time to present a review of some apparent relationships between production and environmental conditions. These can serve as an interim basis for the production of stocks, and as a guide to the kind of observations which will make for better prediction in the future.

To start with, three facts are obvious. First, within limits, more eggs will give more young fish and hence a bigger catch. Second, the adults must get into fresh water to deposit the eggs. And third, large-scale destruction of the deposited eggs by floods will also reduce the populations when the stream bottoms are torn up and eggs and alevins washed out.

The important influence which freshwater factors have on production of salmonid fishes is well documented in North America and in Europe. Some papers are Anon. (1951), Brett (1951), Davidson and Hutchinson (1943), Davidson *et al.* (1943), Fielding (1910), Hagman (1938), Huntsman (1938), Järvi (1945), McKernan *et al.* (1950), Moffett (1949), Murphy (1952), Neave (1949, 1953a, b), Neave and Wickett (1949), Pritchard (1936, 1947a, b), Silliman (1950), Smoker (1953), Wickett (1951, 1952, 1954, in press). Ocean factors are also variable, but

the major and most frequently occurring causes of reduced stocks are close to home. Freshwater conditions and the number of eggs deposited in fresh water are the dominating factors in the majority of cases; ocean conditions impose some additional variation *after* the other factors have set the general population level.

In the five sections below we will consider some of the major causes of death in fresh water. Variation in sea mortality is considered briefly in the Discussion.

I. EFFECTS OF LOW WATER LEVELS ON THE MIGRATION OF ADULTS AND DEPOSITION OF EGGS

The effect of this factor is similar to an alteration in the number of eggs carried by the spawning population. The agencies of death are (1) excessive density of spawning, such that early redds are dug up or the eggs are crowded, (2) failure of the adults to reach productive portions of the stream, (3) death of or excess stress on adults so that eggs are not deposited successfully, (4) increased predation on adult fish because of shallow water and crowding.

The following examples do not prove that every drought will kill or damage fish but they provide strong circumstantial evidence that this has happened, and indicate at least one agency of death. Proof will have to be provided by controlled experiments on stress.

1. NORTH COAST PINK SALMON, 1925, 1930, 1945 AND 1951

Page 59 of the Annual Report of the Canada Department of Fisheries for 1925-26 reads as follows:

The season 1925 was a most difficult one owing to the lack of rain. The season was the driest for many years and this resulted in there being not sufficient water in the streams for the salmon to pass up to the spawning areas in many cases.

Following this, the odd-year pink runs dropped in 1927 to a low level from which they did not recover until 1945 in the central area of the British Columbia coast, and from which they have not yet completely recovered on the Skeena (Neave, 1953a, and later statistics).

On page 53 of the Report of the British Columbia Department of Fisheries for 1930, we read:

At Babine Hatchery there had been only 3.96 inches of rain from April 1st to September 1st making it one of the driest seasons on record.

In the same year, 1930, the August rainfall at Prince Rupert was 0.82 inch, compared with an average of 5.47 inches; and low August rainfalls were also recorded from the Queen Charlotte Islands to Quatsino on Vancouver Island. There were good supplies of spawners, but they could very well have been as ineffective as the spawners that overcame the Babine River rock slide (Godfrey *et al.*, 1954). Brett (1957) discusses this matter more fully. This factor, poor late summer rainfall, is the most likely reason for the drop of the *even*-year pink salmon stocks, in 1932, from which neither the Skeena nor the central areas have yet recovered.

Neave and Wickett (1949) show that late summer rainfall is of importance every year for the populations of statistical Areas 6, 7 and 8 (Fig. 1, Table I). For the spawning years 1928 to 1950, there is no very close relationship between stocks (catch plus spawners) and the number of spawners two years previously ($r = 0.3829$), nor is there a significant linear relationship between stock and July-plus-August rainfall at Ocean Falls two years previously ($r = 0.1651$). The relation between the quotient (stock/spawners) and rainfall is fairly well described by an inverted parabola, suggesting that while increased rain is beneficial up to a point, too much rain is unfavourable. The square of the rainfall was accordingly used as another variate and the following multiple regression equation developed:

$$\text{Predicted stock} = 5.8(\text{rainfall}) - 0.15(\text{rainfall})^2 + 1.3(\text{spawners}) - 42.4$$

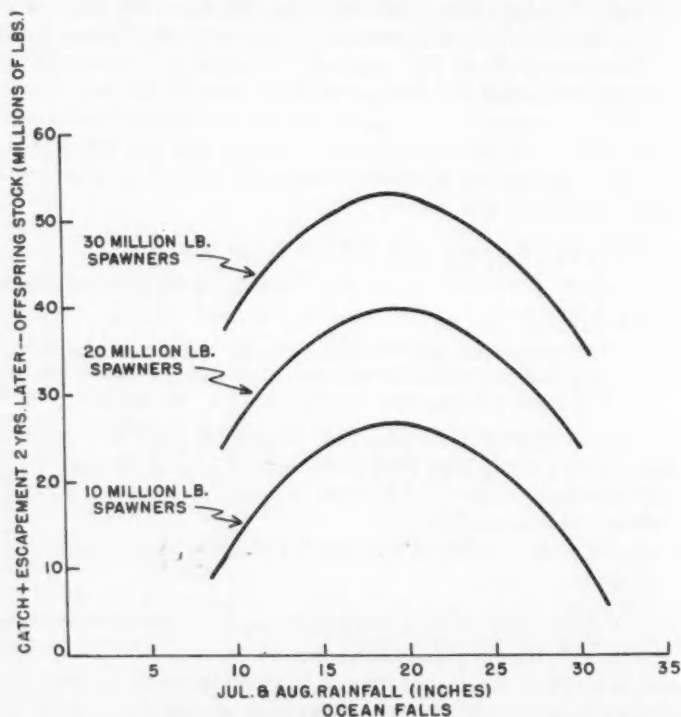


FIG. 1. Variation in mean size of adult pink salmon stock with rainfall (discharge) at the time of adult migration into the streams, computed for three levels of spawning population using the expression on page 1106. Data for the relationship used are from Areas 6, 7 and 8 in the central part of the British Columbia coast for the years 1928-1950. Spawning populations have been estimated from the reports of the Area Director by making "light" equal to 10 million lb., "medium"—20 million lb., "heavy"—30 million lb.

TABLE 1. Rainfall for July plus August at Ocean Falls, coded values of the square of the rainfall, the estimated weight of spawners and the resulting weight of the pink salmon stock in Areas 6, 7 and 8 for the year classes 1928 to 1950 used in calculating the curves of Fig. 1. Data for the years 1951 to 1957 with predicted values of the stock are included for comparison with the more refined data for Areas 7 and 8 in Table VI.

Year of spawning	Rainfall	Square of rainfall	Spawners	Stock	Predicted stock
	<i>inches</i>	<i>in.²/10</i>	<i>10⁶ lb.</i>	<i>10⁶ lb.</i>	<i>10⁶ lb.</i>
1930	5	3	33	17	
1942	7	5	20	30	
1936	8	7	22	23	
1947	10	10	19	38	
1945	10	10	32	27	
1933	10	11	24	27	
1939	11	12	27	29	
1935	11	13	20	31	
1938	12	13	17	13	
1949	13	18	25	40	
1931	14	18	17	32	
1950	14	19	21	40	
1941	14	21	25	56	
1934	17	29	24	36	
1946	17	30	20	30	
1928	19	38	32	63	
1932	20	42	13	33	
1943	21	44	35	59	
1948	24	59	19	32	
1937	25	63	24	38	
1940	27	71	10	25	
1929	28	81	25	22	
1944	29	86	20	27	
MEAN	15.9	30.6	22.8	33.4	
1951	7	5	21	15	29
1952	11	11	25	30	37
1953	13	18	10	19	19
1954	11	11	22	39	33
1955	18	34	14	23	33
1956	10	10	24	...	32
1957	17	29	19	...	38

(1) The size of the spawning populations was taken from the reports of the Chief Supervisor of Fisheries, giving them arbitrary numerical values on a scale of 7. Very Light or #1 was put equal to 5 million pounds of fish. Very Heavy #7 was put equal to 35 million pounds. A continuous record of this type made by experienced officers gives the trend from year to year. (2) Rainfall is the total rainfall in inches for the months of July and August at Ocean Falls. (3) Stock (catch plus escapement) is measured in millions of pounds. Catch data were taken from a special report of the District Supervisors to the Fisheries Research Board, Nanaimo, in 1947 and subsequent years.

The multiple correlation coefficient, $R = 0.7659$, is significant at the 1% level; and its square, 0.5866, indicates that a little less than 59% of the variation in stock size has been accounted for. (The value of R is a measure of the closeness with which the stocks follow rainfall and the number of spawners; a value of 1 would mean perfect correspondence.)

The drops in pink salmon stock from 1945 to 1947, and from 1951 to 1953, are partially explained by the above relationship. In 1945 Dr. F. Neave and the writer made surveys of several streams in the area and were told by Fishery Inspector (now District Supervisor) R. Edwards that very heavy glacial silting had driven the pinks back out of the Bella Coola River into salt water for a time, and when they re-entered the spawners were concentrated in the lower reaches instead of getting to good spawning areas 40 miles upstream. This is a special factor which may be related to run-off.

In 1951 another factor was present that will be treated below (p. 1113), but the following quotation is also pertinent, taken from page 16 of the Report of the British Columbia Department of Fisheries for 1951:

In considering the size of the chum salmon pack and to some extent the pink pack in the Central Area for 1951, the reader must take into consideration the extremely dry weather conditions which prevailed in this area for most of the fishing season. Most of the streams were below normal and as a consequence, pink and chum salmon found it difficult in many cases to ascend the streams to spawn.

2. QUEEN CHARLOTTE ISLANDS CHUM SALMON, 1925

Dr. A. L. Pritchard's reports (on file at the Nanaimo Station of the Fisheries Research Board) concerning pink and chum salmon in the Queen Charlotte Islands, give a valuable picture of the years from 1928 onward. The following quotation is from page 1 of his "Report on the investigation into the life history of the chum salmon (*O. keta*) in the summer of 1929" (our italics):

On the east coast of Moresby Island, which usually produces the most chum salmon on the islands and is considered one of the best areas in the province, the run was a failure when compared with that which usually obtains. The packs of the various canneries were reduced almost to half, with the result that very few of them were able to do more than pay their expenses.

Such a condition might have been predicted. Since the chum salmon spawning streams on the Queen Charlotte Islands are for the most part short, the intensive fishing has always tended to reduce the numbers of fish therein very quickly. This factor, coupled with that of *the very dry season of four years ago* [1925], has been, no doubt, operative in decreasing the run to such alarmingly small proportions, at least in the case of Moresby Island. On Graham Island, the fishery has only been carried on for this species since 1926. Since the chums here are mainly four years old, the factor of heavy fishing will not be felt yet. That *the unfavourable season of 1925, however, took its toll, is evidenced by the small catch of 5000 chums by one cannery* [in 1929], fishing 4 seine boats all season.

3. VANCOUVER ISLAND CHUM AND PINK SALMON, 1952

Over ten years ago Fishery Guardian C. C. Heather told me that his experience had been that drought along southeastern Vancouver Island had at times prevented chum salmon from entering the streams. This had led to the death of particularly large numbers of fish during a season some years prior to 1946, possibly 1935 or 1936.

These observations assume significance in the light of recent events. The low ebb of the southern British Columbia chum salmon stocks recently has raised questions as to the historical background of such changes in production, and the

immediate and long-term prospects of the chum fishery. The major events affecting chum population size in this district appear to occur in fresh water. Pink salmon have a similar freshwater history and exhibit similar dependence on freshwater conditions, though different timing and distribution often give different variations in population size in parts of the area in a particular year.

An immediate cause for the present situation can easily be found. It was one of those natural large-scale catastrophes which escape general notice because of their negative nature—the 1952 drought.

Dr. Neave's photograph of a spawning ground (Neave, 1953b) shows dead *unspawned* chum salmon in Nanoose Creek in November, 1952. During the fall of 1952 Dr. Neave and the writer gathered first-hand knowledge of the extent of low water conditions on both coasts of Vancouver Island. Fishing effort that year had been light because of a strike, but the escapements were not excessive. Streams were low during the whole autumn, with the normal rise of water coming at least a month late.

In a special foreword to the 1952 Salmon Spawning Report, the Area Director, Mr. A. J. Whitmore, wrote:

Adverse low water levels in the streams of Vancouver Island and the lower coast of the mainland, resulting from the lightest rainfall during the months of October and November for many years, interfered with and retarded the normal escapement of the latter part of the pink salmon run and the early portion of the chum runs for a prolonged period beyond the usual time these fish enter the streams.

Pink salmon live 2 years and most of the chums 3 or 4 years. The 1954 pink catches and the 1955 and 1956 chum catches along the east coast of Vancouver Island and the lower mainland dropped from previous levels. The 1952 chum escapement was estimated, in the same report, to have been small in the above area. Hence the very small 1956 chum population can be explained by poor survival of a small number of eggs.

One reason why salmon die under such conditions was found the previous year (Anon., 1951). Pink salmon died in the Tsolum River at Courtenay during the middle of September from scarcity of oxygen. Water at a foot below the surface of pools in the intertidal zone had an oxygen content of 2.45 mg./l. and a temperature of 17.6°C. Action by the Fish Culture Branch to create a temporary barrier and a rise of river flow prevented excessive loss to that particular escapement.

4. NILE CREEK CHUM SALMON, 1946–1949

Nile Creek had a counting fence at the mouth from 1945 to 1953 and a second fence 1,200 feet upstream from 1946 to 1949. The movement of fish into the stream through the first fence was affected by strong southeast winds and, because of small numbers of fish, by the availability of fish in the estuary. A close relationship between discharge and fence count is therefore not present. The spread of the fish upstream does appear to be partly related to discharge during the whole period the run was in the stream, as indicated by the number of chums which entered each fence during October and November, shown in the schedule below:

	Total count Fence No. 1	Total count Fence No. 2	Percentage at No. 2	Mean gauge height at Fence No. 1
	<i>no.</i>	<i>no.</i>	<i>%</i>	<i>feet</i>
1946	1893	236	12.4	0.88
1947	1009	52	5.2	0.43
1948	458	51	11.1	0.74
1949	927	98	10.6	0.80

The importance of density is discussed in Section IV.

II. REDUCTION OF POPULATION SIZE BY EXTREME FLOODS

Floods have long been recognized as a cause of death of eggs and the reduction of succeeding generations. The stream bottom is scoured, and eggs and young fish are found washed onto the banks and out into the estuaries. Trout and birds can be taken with stomachs full of eggs after excessive floods.

1. The floods of 1917 in northern British Columbia caused great damage. The low pink population in 1919, low coho in 1920 and low sockeye population in 1921 were explained this way in Department of Fisheries reports.

2. Neave (1953b) noted that the extremely poor chum fishing season of 1944 in the waters around Vancouver Island can be related to exceptionally severe floods occurring in the autumn of 1940. Examination of the records of the Campbell River shows that very large discharges between October and March occurred in the years 1934-35, 1939-40, 1940-41, 1941-42 and 1953-54. The middle three have been discussed by Neave and Wickett (1949). Five-year-old, 4-year-old and 3-year-old fish of the 1944 stock had been subjected to flooding while in the gravel. There is the possibility that populations originating in 1953 may also have been damaged by floods. The data are less reliable since 1952 because the Amazon has not been gauged and the Campbell River has been regulated more, for hydro-electric power.

3. The Area Director of Fisheries stated in the foreword to the 1955 spawning report that flood damage to pink and chum salmon spawn occurred in the lower Fraser Valley in that year. A reduced pink salmon escapement in tributaries of the lower Fraser River in 1957 can be the result of this damage.

DISCUSSION

The question arises, if droughts and floods have always been reducing chum salmon spawning success from time to time, why is it only now that poor supplies are attracting wide attention? Were water conditions less extreme formerly? did really poor years not occur? or did they merely fail to attract much attention when they did occur? The answer to all three questions may be a qualified "yes". (1) As far as rainfall is concerned, droughts and floods were apparently no less frequent and no less severe prior to 1940 than they have been recently, but modifications of vegetative cover may have made to-day's extremes more harmful to spawning salmon, especially in the southern part of the province. Furthermore, with the present higher level of utilization, a dried or scoured stream does not as quickly regain its former complement of spawners, since a larger percentage of

the stock is taken by the fishery. (2) Hoar (1951), after reviewing the available chum salmon catch statistics, found indications of periods of poor catch in the early years of three successive decades, the 1920's, 1930's and 1940's. Unfortunately changing economic conditions prevented a straightforward interpretation, but he felt that the poor catches were, in part at least, a reflection of scarcity of fish. (3) Whether or not in former periods of chum scarcity there were as few fish as in the 1956-57 period, the effect of a scarcity on the fishing economy was much less serious then. Prior to World War II the salmon industry still concentrated on sockeye and pink salmon as the big money makers. Considerable quantities of chums were taken, where available, but both the price to fishermen and the wholesale price were so low that scarcity of the fish was not a major tragedy. During the war and in the early post-war period values rose and the rate of utilization of chums increased greatly—the present money price to fishermen being more than 10 times the pre-war figure. Whole new fisheries have developed, notably that in Johnson Strait. Under present-day conditions a scarcity of chums becomes very serious, and is reflected in the very widespread concern throughout the industry.

III. WATER LEVELS DURING EARLY STAGES OF INCUBATION AND THE SURVIVAL OF DEPOSITED EGGS

This factor produces variations in survival rates from year to year. It may be the dominant factor at higher deposition densities. Changes in size of the offspring stock are related to water levels during the early stages of incubation. The causal relationship is the change in the flow of oxygen-bearing water in the gravel past the eggs. Wickett (1954) showed that the rate of flow in standpipes set in the gravel was directly related to gauge height of Nile Creek. He also reported (in press) survival of eggs in the standpipes that were consistent with different oxygen supplies. Experimental results (*loc. cit.*) in two columns of eggs through which the water flow was controlled, showed that at a velocity of 1,000 cm./hr. 60 layers of eggs survived, while at 8 cm./hr. only 2 layers of eggs survived. The latter value was in good agreement with the calculated figure, 2.4, derived from the formula (Wickett, 1954) which links oxygen demand of an egg mass to oxygen supply at various velocities and to oxygen contents of the perfusing water.

Examples of the apparent effect of water flow during incubation on pink and chum populations are given below.

1. SKEENA RIVER PINK SALMON, 1951-1955

The combined October rainfall for Prince Rupert, Kitimat and New Hazelton exhibits a direct relationship with the quotient of stock in the offspring year divided by the spawners in the brood year (Fig. 2). Catch is taken from the Department of Fisheries annual statistics, and spawners from their spawning report (Form BC 16). The large 1957 catch in the area appears to be the result of a moderate escapement meeting good incubating conditions in 1955. The 1953 conditions were very good for the escapement of that year. The prospects for 1958 are not as good in comparison (Fig. 2, Table II; see also Wickett, in press).

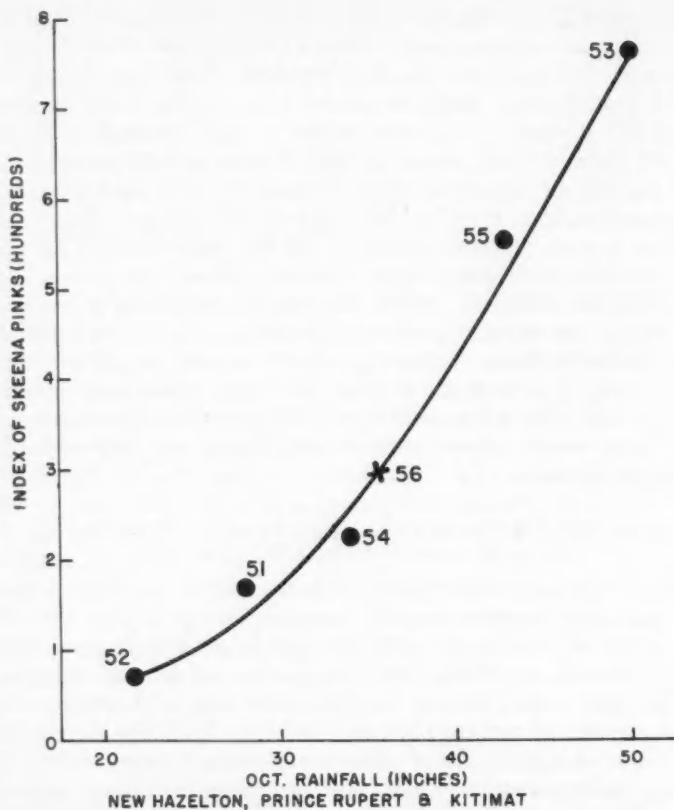


FIG. 2. Index of production ($100 \times$ stock/spawners) for Area 4 (Skeena) pink salmon for the years 1951-1955, and total October rainfall at 3 stations in the area. Survival of eggs from the spawners appears to be influenced by discharge during early incubation.

TABLE II. Data on Skeena River, Area 4, pink salmon for the 1951-1955 year-classes. The production index (column 5) is equal to the stock two years later, multiplied by 100 and divided by the number of spawners. The October rainfall is the total of three stations in the lower Skeena region, Prince Rupert, New Hazelton and Kitimat. The data are graphed in Fig. 2.

Year	Spawners	Catch	Stock	Production index	October rainfall
	10^3 fish	10^3 fish	10^3 fish		inches
1951	399	452	851	174	28.18
1952	1513	1451	2964	72	21.59
1953	269	426	695	763	50.14
1954	349	739	1088	227	34.11
1955	723	1330	2053	550 ^a	43.13
1956	375	416	791	...	35.79
1957	1000 ^a	3000 ^a	4000 ^a

^aPreliminary data.

2. CENTRAL AREA PINK AND CHUM SALMON, 1947-1955

Discharge data for Hooknose Creek at Port John are available since 1947. The quotient (stock/spawners) for the combined areas of Bella Bella and Bella Coola (Areas 7 and 8) shows a direct relation with the November discharge of the river (Fig. 3, 4). The drop from 1951 to 1953 in pinks and from 1951 to 1955 in chums is explained partially by low water. Much spawning takes place in side

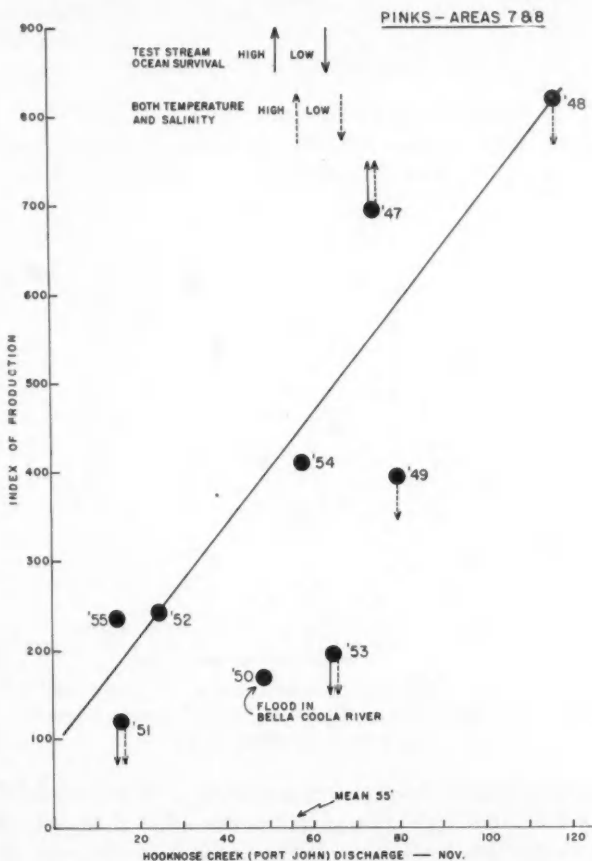


FIG. 3. Index of production for Area 7 plus Area 8 pink salmon for the years 1947-1955, and the mean November discharge of Hooknose Creek. Trend line has been drawn by eye, using the data of Table VII as a guide to aberrant values. The indices in the years 1947, 1951 and 1953 are associated with aberrant values of return from the sea in Hooknose Creek; this is indicated by the solid arrows, which point in the direction that the points in question would be shifted by the action of this factor. The corresponding relation to June sea temperature and salinity is shown by the broken arrows (see Table VII).

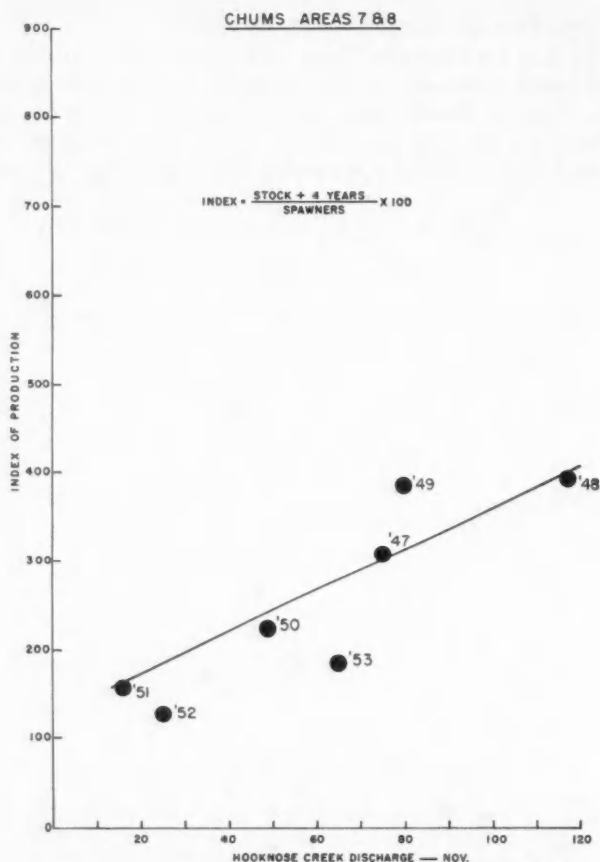


FIG. 4. Index of production for chum salmon, of Areas 7 and 8, assuming all fish return as 4-year-olds, plotted against November discharge of Hooknose Creek.

streams of the large glacial rivers and in numerous small streams of these Areas. The stream at Port John itself appears to be more affected by spawning density than by the water levels (Neave, 1958). Area 7 is the one area of the coast where spawning densities have increased in recent years, as indicated by data supplied by the Fishery Inspectors. As noted below, it is at the higher densities that percentage survival of eggs in the gravel is likely to be the dominant factor in production.

3. VANCOUVER ISLAND (DISTRICT 3) CHUM SALMON, 1926-1947

Fig. 1 in Neave and Wickett (1949) shows the relation between combined mean discharge for the Amazon and Campbell Rivers for the month of November

and the population size of District 3 chum salmon four years later (Fig. 5, Table III). Escapement was taken from the spawning reports of Fishery Inspectors, using the numerical estimation when given and applying numerical values to subjective reports for early years on the basis of the relation of numerical and subjective reports in known years. Catch was converted from weight to numbers of fish using a factor of 10 pounds per fish. Stock is the catch plus escapement, four years after the spawning year. The years of 1934, 1939, 1940 and 1941 are excluded because large floods occurred (see p. 1110). The equation below was computed:

$$\text{stock} = 2.8 + 0.51(\text{discharge})$$

"Discharge" is the sum of the November mean discharges of the Amazon and Campbell Rivers, in thousands of cubic feet per second; "stock" is in millions of fish. The correlation coefficient, $r = 0.7356$, is significant.

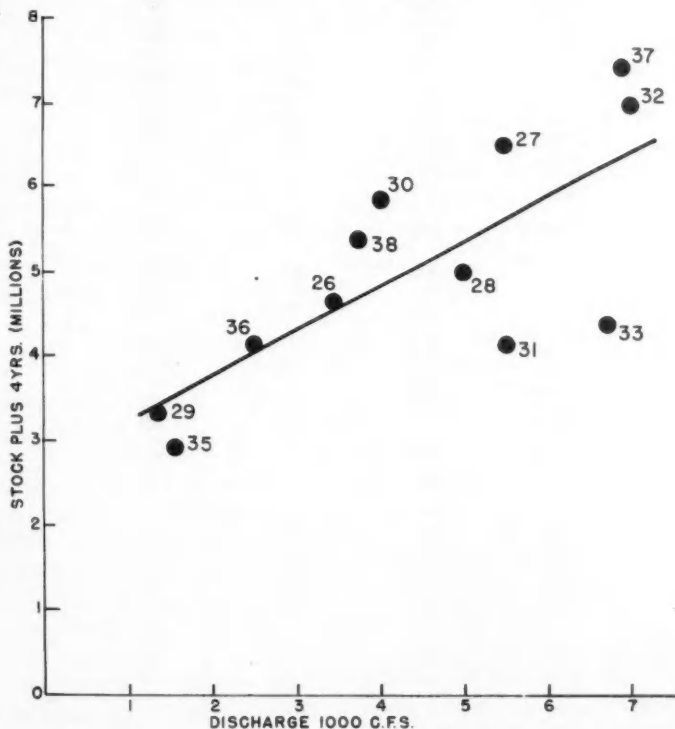


FIG. 5. Relation between stock of Vancouver Island chum salmon and combined November mean discharges of the Campbell and Amazon Rivers 4 years previously, for the years 1926-1938. The mean number of spawners was 2.9 million. During this period there was little apparent connection between number of spawners and resulting stock (Table III).

TABLE III. Total of the Amazon plus Campbell River mean November discharges, the number of Vancouver Island (District 3) chum salmon spawners, and the stock four years later, for the years 1926 to 1952. The number of spawners for 1926-33 was calculated from "subjective" reports; those for the years 1934-56 are from the Inspectors' numerical reports. Catch figures used to calculate the stock are taken from pack and dry-salt weights for 1930-45, from weights supplied by the District Supervisor of Fisheries for 1946-50, and from numbers of fish in the Annual Statistics of the Department of Fisheries for 1951-56. Numbers of spawners only are given for 1953-56, because the Amazon River is no longer gauged and the Campbell River has been increasingly controlled for hydro-electric power.

	Discharge	Spawners	Stock 4 yrs. later
	10 <i>cfs</i>	10 ⁴ <i>fish</i>	10 ⁴ <i>fish</i>
1926	347	210	466
1927	552	297	648
1928	506	322	500
1929	134	315	334
1930	406	274	585
1931	552	362	413
1932	708	362	696
1933	668	210	436
1934	905	382	548
1935	160	206	296
1936	250	357	415
1937	685	219	740
1938	375	310	541
MEAN	445.2	286.6	509.1
1939 ^a	1408	147	221
1940 ^a	366	220	116
1941 ^a	550	325	295
1942	364 ^b	273	533
1943	250 ^b	128	464
1944	638 ^b	77	427
1945	253 ^b	120	359
1946	158 ^b	272	595
1947	336	195	553
MEAN	333	177.5	488.5
1948	455	135	310
1949	801	210	468
1950	544	201	593
1951	359	266	186
1952	298	203	226
MEAN 1942-52	405.1	197.7	428.5
1953	...	199	...
1954	...	242	...
1955	...	103	...
1956	...	106	...
MEAN 1942-56	...	188.5	...

^aYears of floods.

^bAmazon discharge estimated.

A multiple correlation coefficient which includes the size of the spawnings only increases the fourth decimal place of the correlation, from $r = 0.7356$ to $R = 0.7359$, so that before the floods of 1939-1941 numbers of spawners does not appear to have been a limiting factor. Stream discharge in early winter resulted in varying survival rates, and these showed up mainly in the size of the stocks four years later. Hoar (1951, p. 34) found, in calculating his "index of return" the effect of any likely variation in age composition would not appreciably affect comparisons of parent and progeny generations in the above period. A four-year cycle was assumed for the above relation, but as about a third of the chums are 3-year fish, effects of low survival also show up to some extent in the third year after spawning.

For the brood years 1942 to 1947, the Vancouver Island chum salmon populations show a significant relation with number of spawners but not with Campbell River discharge (Fig. 6, Table III—the Amazon gauging station was discontinued):

$$\text{stock} = 3.31 + 0.885(\text{spawners})$$

Stock and spawners are in millions of fish. The spawning populations are much smaller than before, it will be noted (Table III).

In more recent years, the returns from the brood years 1949 and 1950 also follow the above relationship reasonably well. The year 1948 gave a lower than predicted return: this may be from lack of fishing effort in 1952 because of a strike, and from failure of the full escapement to show up on the spawning beds because of drought. The loss of 3-year-old fish may explain, in part, the small population in 1955 after the drought of 1952 which has been mentioned above. The principal effect of the 1952 drought was felt in 1956.

IV. PERMEABILITY OF THE SPAWNING GROUND AND FRY PRODUCTION, IN RELATION TO DENSITY OF EGGS

Permeability is a measure of the ease with which water can flow through any material. Gravel with high permeability allows a higher velocity for a given pressure gradient than a gravel with low permeability. Various pressures will be applied to the water in the gravel of a redd during an incubating season, but the most permeable will usually have the greatest velocity and so carry the greatest supply of oxygen. It was shown by Wickett (1954) that some gravel could carry too little oxygen for the survival of chum salmon eggs. Fluctuating flow in some streams, and poor bottom in streams with steady flow are reported. The first effect has been discussed above. The second situation is the one to be considered here.

An instrument to measure the permeability, velocity and oxygen content of water in gravel was developed by Wickett (1954). This was improved by engineers of the Pacific Oceanographic Group (Pollard, 1955; Terhune, 1958). Reliable results for velocity have been possible since January 1957, using the "Mark VI" standpipe water meter.

Where counts of fry survival have been made for a number of years it is possible to compare average fry survival and average permeability. Nile Creek on

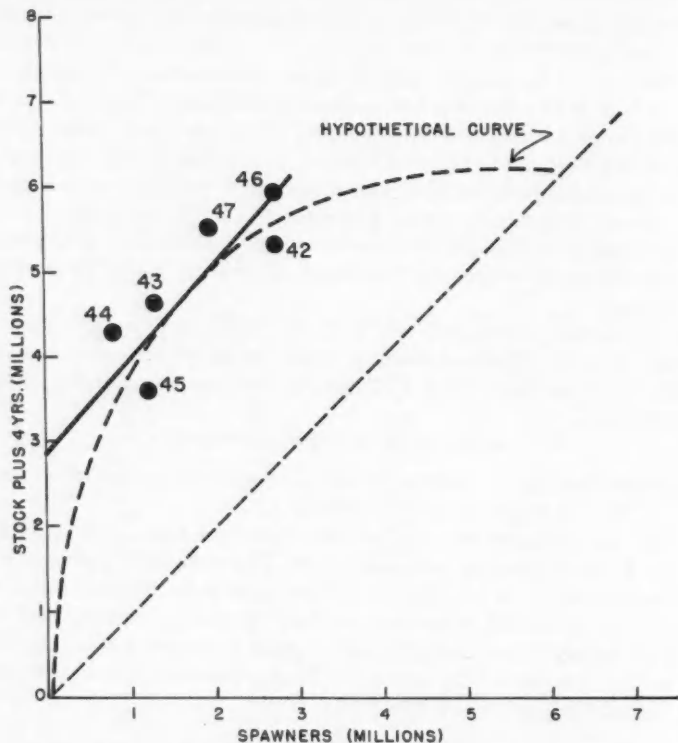


FIG. 6. Relation between stock of Vancouver Island chum salmon and numbers of spawners 4 years previously, for the years 1942-1947, following 3 years which had extreme floods. The mean number of spawners is 1.8 million, 1.1 million less than for the period shown in Fig. 5. The relationship is shown as linear, but is probably part of a curvilinear relation such as that indicated by the broken line.

Vancouver Island and Hooknose Creek at Port John in the Central Area had pink and chum counts made for 8 and 10 years respectively, and stream conditions had not changed greatly up to the time permeability readings were made in 1957. McClinton Creek in the Queen Charlotte Islands was studied from 1930 to 1940 (Pritchard, 1948); the stream bed has not changed character in the intervening years as far as can be ascertained. Morrison Creek on Vancouver Island, tributary of the Puntledge River at Courtenay, was fenced for only two years, 1943 and 1945; it is little if any changed since that time. Survivals of eggs in these streams are given by Pritchard (1947b), Wickett (1952) and in recent Annual Reports of the Fisheries Research Board.

These streams were surveyed for permeability using the Mark VI meter. The average permeabilities corrected to 10°C. (K_{10}), and geometric mean survivals (eggs-in-females to fry) are as follows:

Creek	K_{10}	Survival	Years of observations
Nile	1914 cm./hr.	Chum—1.2%	8
Morrison	3849 cm./hr.	Pink—5.7%	2
Hooknose	4035 cm./hr.	Chum—7.6%; pink—7.2%	10
McClinton	9617 cm./hr.	Pink—13.15%	6

These data suggest that looser gravel gives a higher survival.

HOOKNOSE CREEK. Neave and Hunter (unpublished) have found that Hooknose Creek's output of pink and chum fry is mainly determined by the combined density of spawning adult fish. More fry are produced up to a density of 0.6 fish per square yard of stream bottom, measured bank to bank. 1,409,000 fry were produced from 9,556 spawners in an area of 16,800 square yards. Hunter (unpublished) estimated that 7,500 square yards are actually used, which gives a density of 1.3 per square yard.

NILE CREEK. At Nile Creek a similar relationship is found. The stream was fenced near the mouth in all years; in 1945 it was also fenced at a point 1,100 yards upstream, and from 1946 to 1949 at a point 433 yards upstream. In 1945 and 1951–1953 spawning took place throughout the stream. From 1946 to 1949, spawning took place below the upper fence. In Table IV the effects of density are shown.

TABLE IV. Total pink and chum salmon fry output per unit area of total stream bed, at various densities of total pink and chum spawners in Nile Creek on Vancouver Island. Adult and fry counts were not made in 1950–51. The data are graphed in Fig. 7.

Year	Spawners	Fry	Area	Spawners	Fry
	no.	no.	sq. yd.	no./yd. ²	no./yd. ²
45–46	3,062	131,451	30,800	0.99	4.3
45–46 ^a	2,841	120,540	8,040	0.35	15.
46–47	1,663	8,859	3,600	0.46	2.5
47–48 ^b	949	4,808	3,600	0.27	1.3
48–49	407	23,241	3,600	0.11	6.9
49–50 ^b	835	929	3,600	0.23	0.3
51–52	338	23,195	30,800	0.01	0.75
52–53	1,649	109,887	30,800	0.05	3.5
53–54	114 ⁺	18,804	30,800	0.004 ⁺	0.6

^aOnly the part of the run between the fences is considered.

^bYears of severe floods.

Large floods took place in 1947–48 and 1949–50 so that the production of these spawnings is low. The rest of the years exhibit a domed relation between density of spawners and the fry output per unit area, with the maximum output probably at a density a little less than 0.35 (Fig. 7).

MCCLENTON CREEK. For McClinton Creek, the area of spawning ground measured bank to bank is 110,000 square yards. The area covered with water has been estimated at 42,000 square yards. The maximum output of fry was made at densities of 1.4 spawners per square yard bank to bank, or 3.7 per usable square yard. The latter value assumes a width of 10 yards. The stream is reported narrower than this during part of the spawning season. Very high densities can

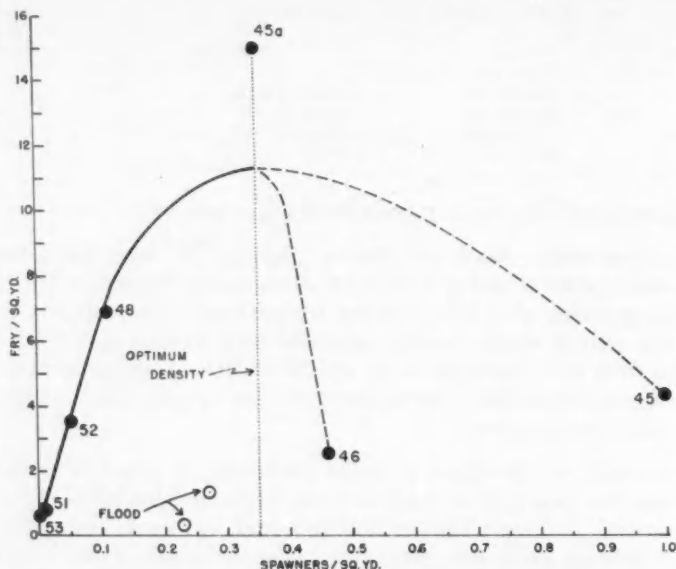


FIG. 7. Relation between density of spawning pink and chum salmon at Nile Creek and the total number of pink and chum fry produced per square yard of stream bottom. The points are erratic above 0.35 fish per square yard, and at these densities are probably strongly influenced by environmental factors such as that shown in Fig. 5 for the whole region.

be tolerated in permeable gravel. Dr. Pritchard noted, in the above-mentioned reports, that in 1930, for which we calculate densities of 0.6 fish (bank to bank), or 1.6 (fish usable) per square yard, the actual density was 6 fish per square yard at the place where densest egg deposition was taking place.

RATING CURVE. From these data, as shown in Table V, it would appear that we are being conservative if we use the density from the bank to bank measurements of Nile, Hooknose and McClinton Creeks to draw a "rating curve" for relating average permeability to optimum density. The data from the "Spawners" column plotted against K_{10} give a straight line passing through the origin (Fig. 7). This is what would be expected if the rate of flow of oxygen-bearing water were the principal factor governing survival, because (1) D'Arcy's Law shows that permeability and velocity are directly related, for a given pressure gradient, and (2) Wickett (1954, in press) has shown that the number of layers of eggs in an egg mass that can survive without stress is directly related to the velocity.

When usable area is substituted for bank-to-bank area in estimating fish density, the three upper points and broken (freehand) line of Fig. 8 are obtained. In this restricted area of Nile Creek the average permeability is greater, but the other two creeks are not affected.

MORRISON CREEK. Morrison Creek has a mean survival value somewhat above the rating curve of Fig. 8, but only two years of survival were measured: 4.7% and

TABLE V. Average permeability at 10°C. in centimetres per hour (K_{10}), density of spawners that produced most fry, and maximum fry production per unit area, in three test streams. The data are presented in terms of total area of spawning grounds (bank-to-bank width), and in terms of area of gravel actually used. They are graphed in the form of an efficiency rating curve in Fig. 8.

Creek	K ₁₀	Spawners which give maximum fry		Maximum fry
		cm./hr.	no./yd. ²	no./yd. ²
A. BASED ON BANK-TO-BANK AREA				
Nile	1914	0.35	15	
Hooknose	4035	0.6	83	
McClinton	9617	1.4	114	
B. BASED ON AREA USED				
Nile	3526	2	87	
Hooknose	4035(?)	1.3	188	
McClinton	9617(?)	3.7	300	

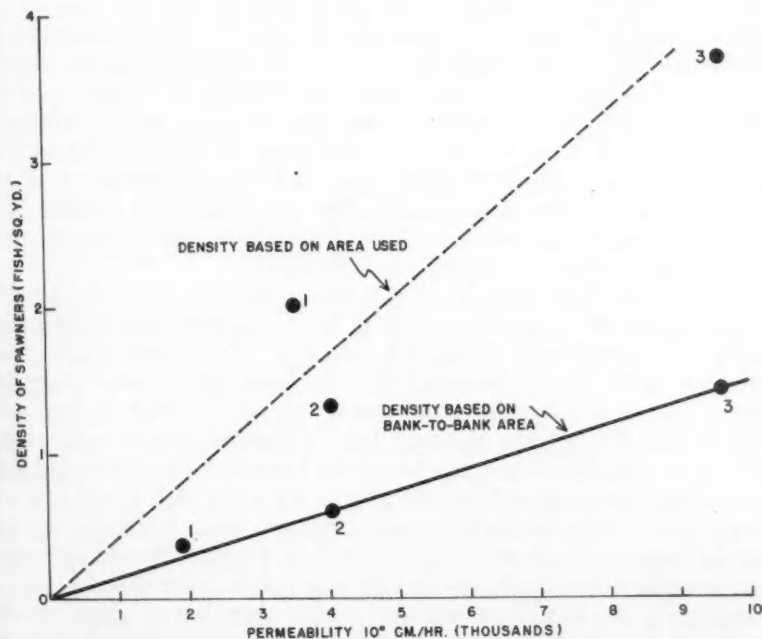


FIG. 8. Densities of pink and chum spawners that produced the approximate maximum numbers of fry in three test streams of the British Columbia coast, and average permeabilities of the gravels in those streams. The solid line shows density based on areas calculated from the bank-to-bank average width. The dotted line is based on estimates of areas and permeabilities of areas actually used by the spawning fish.
1—Nile Creek; 2—Hooknose Creek; 3—McClinton Creek.

6.7%. The density of spawners was 1.3 per square yard for the 4.7% survival, and 1.1 per square yard for the 6.7% survival. Since the smaller of the two spawning runs produced the larger number of fry, it may be that both spawnings were above the level which produces maximum fry. In any event this level cannot be determined from only two observations, and this creek was not used in establishing the rating curve above.

DISCUSSION

The changes in survival rates can be so great, due to the normal variation of the environment, that prediction for long periods will depend upon improved climatic forecasts made for years ahead. Short-term prediction should become possible after an assessment of freshwater conditions after the fry have left the streams.

Number of spawners is basic to all prediction. The spawning stock must be kept as close to the optimum density as possible if large populations are to exist. This density can be determined by a study of the stream gravels and an examination of the numbers which have produced the largest (average) returning stock.² A density of 0.3 spawners per square yard is needed in Nile Creek for maximum output of fry, and this stream has poor gravel. Only 5 statistical areas of the coast have averaged as many as 0.3 spawners per square yard in the period from 1951 to 1955. Three of these areas are in the Queen Charlotte Islands, where a test stream (McClinton Creek) has shown that 1.4 fish per square yard are needed for maximum fry output. The average densities and range of densities of spawning pinks and chums have been calculated for all the statistical areas of the coast from data supplied by Fisheries Inspectors through the courtesy of the Area Director A. J. Whitmore (Table VI). Data for 445 out of a possible 1,115 streams have been used. These preliminary data indicate that greater numbers of spawners can be used to advantage, in most places.

No mention has been made above of variability in ocean survival. Estimated adult stock produced by known numbers of fry at Hooknose Creek has varied from 0.7% to 5.2% over 9 years (Table VII, column 8). The maximum is 2.4 times the geometric mean, and the minimum 0.27 of that mean. There is some suggestion that survival is related to temperature and salinity in the ocean in June (the month just after the fry enter the sea), low temperature and reduced salinity being unfavourable. Of course it may be another factor or factors associated with these two that are actually unfavourable, but in any event such a correlation, if confirmed, would imply that in this area variations in ocean survival mostly are determined within a month or two of the time the fry enter the sea. However, this one example can only be suggestive, and be a lead for further study.

Considering a whole statistical area, rather than just a single stream, variation in ocean survival might be somewhat less than 7:1 observed at Hooknose Creek over 9 years (see Fig. 3), particularly since the Hooknose returns include any effect of a (possibly) variable rate of removal by the fishery.

²The density which gives maximum stock is a little greater than that which gives maximum yield.

TABLE VI. Range of density and weighted mean density of pink and chum salmon (in number of fish per square yard) in the Statistical Areas of the British Columbia coast for the years 1951-1955. Preliminary data for 445 out of 1,115 streams supplied by Inspectors of Fisheries through the courtesy of Area Director A. J. Whitmore.

Area	Chum Salmon		Pink Salmon		Both species
	Range	5-year av.	Range	5-year av.	
1	0.09-0.39	0.22	0-0.94	0.45	0.67
2B, E & W	0.04-0.56	0.26	0-0.64	0.14	0.40
2A	0	0	0.11-0.71	0.41	0.41
3	0.01-0.19	0.08	0.04-0.25	0.13	0.21
4-1	0.0003-0.02	0.007	0.04-0.39	0.15	0.157
4-2	0.0005-0.005	0.002	0.08-0.67	0.21	0.212
4-3	0.001-0.005	0.0035	0.0035
5	0.015-0.06	0.03	0.05-0.11	0.10	0.13
6	0.02-0.11	0.05	0.02-0.14	0.08	0.12
7 ^a	0.74-1.74	1.36	1.11-1.76	1.51	2.87
8	0.02-0.09	0.07	0.10-0.30	0.15	0.22
9	0.002-0.05	0.02	0.005-0.05	0.02	0.04
10	0.009-0.03	0.02	0.007-0.07	0.035	0.055
11 & 12	0.06-0.09	0.07	0.03-0.09	0.05	0.12
13	0.02-0.17	0.08	0.12-0.56	0.27	0.35
14	0.07-0.17	0.10	0.03-0.13	0.09	0.19
15	0.01-0.03	0.017	0.00007-0.02	0.008	0.024
16	0.03-0.13	0.07	0.001-0.42	0.12	0.16
17	0.05-0.12	0.07	0.003-0.03	0.006	0.076
18	0.01-0.10	0.04	0	0	0.04
19 & 20	0.20-0.31	0.26	0	0	0.26
20-23	0.07-0.30	0.19	0-0.01	0.0036	0.2036
24	0.12-0.43	0.26	0-0.002	0.0015	0.2615
25	0.015-0.025	0.02	0-0.01	0.004	0.024
26	0.04-0.12	0.08	0-0.01	0.0053	0.085
27	0.02-0.10	0.06	0-0.31	0.11	0.18
28	0.006-0.03	0.02	0-0.03	0.01	0.03
29 ^b	0.001-0.02	0.01	.000004-0.03	0.01	0.02

^aIn this Area the stream area is that used by the fish, rather than from bank-to-bank measurement. There are only 4 years' data for this Area.

^bStreams tributary to the lower Fraser River.

Floods in winter or drought at migration time can make the stock less than the original number of spawners. At the other extreme, favourable discharge during incubation can allow increases up to 800% if the other two factors are also favourable (Fig. 3-1948). Above this, the best observed ocean survival (at Hooknose Creek) was 2.4 times the geometric mean. Hence exceptionally favourable ocean conditions *could* increase survival to practically 2,000% of the spawners.

An increase of this order will be achieved only rarely, because it requires at least *four* environmental factors to be favourable concurrently. The average production will be closer to the lower limit than the upper, because any one of the three critical freshwater factors can, by itself, impose low survival.

An important conclusion is that no influence not already recognized is needed to explain the large fluctuations in stocks of pink and chum salmon that have been observed recently.

A second conclusion is that really large stocks can only come from near-optimum numbers of spawners. In most areas optimum numbers are much greater than the present numbers.

TABLE VII. Pink salmon production and ocean survival on the central coast of British Columbia. Columns 2-4 present data for Areas 7 and 8. During this time extreme values of July-plus-August rainfall have not occurred (column 5). Stock (column 3) is estimated as equal to catch plus escapement. The production index (column 4) is column 3 as a percentage of column 2. November rainfall at Ocean Falls (column 6) is given for comparison with Hooknose Creek November mean discharge (column 7). Column 8 gives the number of spawners returning from the sea to Hooknose Creek on King Island, as a percentage of the number of outgoing fry. Deviations from the long-term mean salinity (ΔS) and deviations from mean temperature (ΔT) for the month of June at Ivory Island (near the centre of the combined Areas), in the year the fry enter the sea, are given in columns 9 and 10, from observations of the Pacific Oceanographic Group of the Fisheries Research Board.

1	2	3	4	5	6	7	8	9	10
Brood year	Spawners	Stock 2 yrs. later	Production index	Ocean Falls rainfall July + Aug.	Ocean Falls rainfall Nov.	Hooknose November discharge	Hooknose ocean survival	ΔT	ΔS
	10^4 fish	10^4 fish	%	inches	inches	cfs	%	$^{\circ}\text{F}$	%
1947	390	2714	696	7	15	75	5.2	+1.2	+0.31
1948	497	4081	821	24	29	117	3.1	-1.4	-0.73
1949	1079	4266	395	13	28	80	3.2	-0.9	-1.94
1950	1557	1814	117	14	25	49	3.7	+0.5	-0.90
1951	1162	1389	120	10	16	16	0.7	-2.6	-1.04
1952	802	1931	242	11	12	25	2.6	-0.7	+0.59
1953	681	1338	196	13	26	65(est.)	0.6	-1.4	-2.16
1954	765	3144	411	11	31	58	2.4	-1.6	+1.16
1955	733	1718	234	18	12	15	2.7	(discontinued)	
1956	1157	10	26
1957	1078	17	28
Mean	955	2343	245	16	23			55.1	27.46

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